PALEOBOTANY AND BIOGEOGRAPHY

A Festschrift for Alan Graham in His 80th Year

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A Festschrift for Alan Graham in His 80th Year

W. D. Stevens, Olga Martha Montiel,
and Peter H. Raven (editors)

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FOREWORD

On the one hand, Alan Graham's accomplishments over a botanical career that spans six decades can be measured by the approximately 250 papers and books that he has published during this time. These publications, along with those of his many students and associates, have greatly advanced our knowledge of the floristic history of the New World over the past 75 million years. They have helped us all to gain a better and more precise picture of the complex and ever-shifting patterns of migration, differentiation, separation, and re-aggregation of the plants and plant communities of the region during that long and exceedingly interesting period.

As we honor Alan now on the occasion of his 80th birthday, however, we consider equally significant his 38 years of teaching at Kent State University (1964–2002) and his subsequent 12 years as Research Associate at the Missouri Botanical Garden. I was absolutely delighted when Alan and his wife, Dr. Shirley A. Graham, accepted my invitation to join us at the Missouri Botanical Garden. During the years since they came to the Garden, the Grahams have contributed greatly to our collective scholarly enterprise and helped to maintain the collegial atmosphere of our institution that we all prize so highly.

Over his professional career of more than a half century, Alan Graham has encouraged hundreds of students and colleagues in the study of botany. He has particularly nourished and built the interest of these individuals in the amazing story of how the very different communities and their individual plants that lived in the past gradually evolved into those we see around us at present. While at Kent State University, Alan did an exemplary job of teaching and mentoring students, and at the Missouri Botanical Garden his door has always been open to those seeking to understand and appreciate the plant communities of the past.

It is because of both his very substantial contributions to botany for such a sustained period of time and his generosity and affability that so many of his colleagues enthusiastically agreed to contribute to this volume in his honor. In doing so, they celebrate his fine contributions measured over a productive lifetime as well as his notable friendship and encouragement to so many others laboring in the same or related fields. Alan Graham has mastered the science of paleopalynology and used it to analyze samples of fossil pollen from throughout the Western Hemisphere. Over the years, by communicating so widely and generously with students of problems similar to the ones he took up, he has helped to make the whole field collegial—much more productive than it would have been without his meaningful participation in

it. It is a particular satisfaction that his reference collection of pollen slides is deposited permanently at the Smithsonian Tropical Research Institute in Panama, where it will be directly available to students of the palynology of the living and fossil plants of the Americas.

In the 1960s Alan initiated an innovative long-term study of tropical American vegetation history with the support of the National Science Foundation, producing a valuable series of publications on Neotropical palynology between 1969 and 2001 and a symposium volume on the vegetation and vegetational history of northern Latin America. Initially, he focused on lignites and associated sediments that frequently contained macrofossils, gathering tens of thousands of specimens from throughout Latin America and from the entire Tertiary Period as well as the Late Cretaceous. Integrating the fossil information with data on geology and past climates, and linking the fossils with their descendants in the modern flora, Alan Graham formed a broad synthesis of the ecosystems, phylogenetic history, and biogeography of the Americas. He presented information from these studies in a series of books, including *Late Cretaceous and Cenozoic History of North American Vegetation*, *Late Cretaceous and Cenozoic History of Latin American Vegetation and Terrestrial Environments*, and *A Natural History of the New World*.

Alan Graham has notably demonstrated that lowland tropical rainforest may be geologically recent in many of the areas where it occurs today, and thus that the species in them would logically be of relatively recent origin also. Although prior to 1976, when Alan published his seminal paper on the topic, it was believed that huge stretches of this forest were age-old relicts of the past, it is now clear that they spread extensively as the climate warmed, as continental ice formed around both poles, and as the equator-to-pole climatic and temperature gradient steepened in both Northern and Southern hemispheres. This key finding is consistent with the demonstration that the large clusters of species in many tropical forest groups, even ones with far-flung distributions, are often phylogenetically close and resemble one another greatly in their molecular characteristics. It is also consistent with the observation that the archaic, relictual members of plant families, representing older lineages within their respective groups, are characteristically found in tropical mountains (in Queensland, New Guinea, New Caledonia, Madagascar, and to an extent in the New World in similar habitats) and not in the tropical rainforest itself.

Alan Graham has also made valuable contributions to our understanding of the effects of climate shifts from the Middle Miocene epoch onward (the past 15 million years) on the floras of recently uplifted mountain ranges such as the tropical Andes and on vegetation shifts in the Western Hemisphere generally during this period. Many other periods of time and particular areas have also been the subjects of his analyses, which have uniformly proved useful.

The 14 contributed papers in this volume present much that is original and span the geography that has interested Alan Graham for his entire professional life. Eight of them deal with Latin America, the other six with the United States and Canada. Thus, in one fascinating account, Barreda and Palazzesi demonstrate a rapid transition from forested to shrubby ecosystems in Patagonia during the same mid-Miocene time we have been discussing, consistent with the sharpening gradient for vegetation and climate from the equator to the pole. Simpson, considering the flora of temperate South America, uses phylogeographic analyses to conclude that most of the plant communities and their constituents in the region evolved in situ. There are of course strong, demonstrated linkages of many elements of these floras with those of Australia and New Zealand via Antarctica that indicate migration as well as distance dispersal between these regions, but where the particular elements originated is another and more difficult question.

In Panama, Jaramillo and his colleagues demonstrate a continuity of forest vegetation with what they interpret as Gondwanan-Amazonian taxa for the past 20 million years. It is surprising that this well-studied

sequence does not show a mid-Miocene discontinuity, a relationship that indicates the need for further studies both to the north and to the south to document fully the regional context. Such a context is pertinent to interpretations both of migration between South and North America prior to the uplift of Panama and of the development of lowland rainforest in the region. In another paper, Winterton et al. conclude on the basis of phylogenetic analyses that the legume genus *Dussia* migrated between Central and South America prior to the closing of the Isthmus of Panama, as do Calvillo-Canadell, Cevallos-Ferriz, and Sousa-Sánchez in their description of *Inga* fossils from Nuevo León in the Eocene Period.

For *Oreomunnea*, Herrera et al. report macrofossil evidence of the existence of the genus in the Early Miocene of Panama, speculating on the basis of the modern range of the genus that there may have been considerable uplift in the area at that time. An alternative explanation would be that lowland habitats may have been more like those of the mountains today, a pattern consistent with what we have discussed for the survival of archaic angiosperms in general. Finally, for the northern Andes, Flantua et al. demonstrate radical, elevation-linked shifts in vegetation in the area since the Last Glacial Maximum.

In apparent contrast are the results presented by Magallón and her colleagues on the composition of the lowland tropical rainforest in Mexico during Late Cretaceous to Paleogene time. Their analysis indicates that these forests are not closely related in floristic composition to the lowland tropical rainforests of other regions, but are most closely related to the montane forests of the same region today. This finding implies that most of the ancient forests were derived within Mexico from elements that were present in Laurasia, and not influenced by South America until later times than have more traditionally been accepted.

The remaining six papers have to do with Tertiary Period vegetation in the United States and southern Canada. Several of these discuss taxa that are no longer present in the regions from which they are being reported—*Melia* in the mid-Miocene epoch of central Washington (Pigg et al.), detarioid legumes from the Eocene of western Tennessee (Dilcher et al.), and the extinct fagaceous genus *Catahoulea* from Kentucky, Tennessee, and Texas (DeVore et al.). The loss of *Abies bracteata*, now confined to the Santa Lucia Mountains of California, is used by Leopold and Zaborac-Reed as a basis for understanding the regional extinction of taxa during a period of complex climate changes in the Oligocene of Colorado. Finally, the development of the temperate forests of western North America is illustrated by a study of the Paleocene flora of southern Alberta (Stockey et al.) and by one of the Late Miocene fossils from near the present location of Seattle, Washington (Dillhoff et al.).

All of these papers enhance our knowledge of the particular regions and times treated in the framework of the overall evolution of the vegetation of the Americas. They carry forward or dispute traditional hypotheses of past migrations and of the course of evolution in widely distributed parts of the Americas. Taken together, they not only advance knowledge but also demonstrate closely that the efforts of Alan Graham during the course of his career will carry on for centuries in the future as we find greater clarity and develop even more robust hypotheses of the evolution of the vegetation of the Americas.

Peter H. Raven, President Emeritus, Missouri Botanical Garden, St. Louis, MO, U.S.A.

PREFACE

We take great pleasure in honoring Alan Graham's substantial contributions to the fields of paleobotany and biogeography on the occasion of his 80th birthday. This *Festschrift* contains 14 papers prepared by 56 of Alan's friends and colleagues representing 15 nationalities and working in 27 institutions. The participants do not exhaust the list of people who have collaborated with Alan throughout his long and productive scientific career, or the many students who received their degree under Alan Graham, but the papers they have contributed represent those fields in which Alan has had the greatest impact through his work. During the past five decades, Alan Graham has excelled in the elements that comprise an outstanding academic career: scholarship, teaching and mentoring of undergraduate and graduate students, service, and generosity toward colleagues. Since he and Shirley relocated to the Missouri Botanical Garden in 2002, Alan has been fully engaged in fruitful research and in service to our institution. This book is also intended to express our gratitude for his many contributions to the Missouri Botanical Garden.

The editors would like to give very special thanks to Shirley Graham, who participated enthusiastically in this homage to Alan and also shared many personal notes, which are included in Alan's profile. Dawn Trog, from the Center for Conservation and Sustainable Development (CCSD) of the Missouri Botanical Garden, made important contributions to the organization of the work and to the preparation of the book. Gail Milder from CCSD helped with editing of the front matter. Fred Keusenkothen from the Imaging Lab at the Missouri Botanical Garden helped with editing of the images, and Linda Oestry from the Missouri Botanical Garden Library assisted in obtaining historical images. Allison Brock from the Missouri Botanical Garden Press managed the technical editing with great professionalism and promptness, and Jeanne Ponzetti from Ponzetti Editorial Services & Botanical Consulting diligently conducted the technical editing of the manuscripts. Last but not least, we would like to express our gratitude to all of the contributors for their willingness to participate and for responding with excellent papers that continue to advance the fields of paleobotany and biogeography.

PROFILE OF ALAN GRAHAM

Alan Graham was born and grew up on Lubbock Street in Houston, Texas, the only child of Lyndon and Hattie Stampley Graham. His neighborhood has since become part of the Old Sixth Ward Historic District just across Buffalo Bayou from downtown and contains the largest concentration of preserved mid- to late 19th-century houses in Houston, including several of the "shotgun" style like his home until college days. In the 1940s, the Sixth Ward was an ethnically mixed neighborhood of Bohemian, Italian, and Scotch-Irish working-class immigrants with a small but growing Mexican population. Alan had an early interest in science and writing, which he attributes to the lifelong impact made by three teachers at Dow Elementary and Junior High School: Mrs. Muller in Biology, who believed in understanding through observation and experimentation; English teacher Mrs. Jackson, who believed in the importance of writing grammatically correct and effective sentences; and Mrs. Weaver, who introduced him to an appreciation for all kinds of "good" music. During his elementary school days at Dow, Alan and his two best friends, Sammy Giammalva and Richard Schuette, discovered the public Houston Tennis Courts recently constructed near their homes. Free lessons and encouragement from the Club professional, Robert Nesmith, provided opportunities that were life-changing for the three boys. All of them, first in their families to go to college, attained professional careers, Alan with his Ph.D., Richard with an M.D., and Sammy with a place on the U.S. Davis Cup team and a career in professional tennis. Alan's skills led to city, state, and national tennis awards and entrance to the University of Texas in 1952.

On his graduation from Sam Houston High School, the University of Texas offered Alan the choice of an academic scholarship in engineering or an athletic scholarship in tennis. After what he has called "a singularly unsuccessful one-semester career in ROTC and as a fraternity pledge for Delta Kappa Epsilon," and after greater familiarity with the real world of engineering, he opted for the athletic scholarship with a major in biological sciences, eventually focusing on botany. An energetic new hire to the Botany Department, Dr. Billy Turner, and the stalwart Texas botanist Dr. Benjamin Carroll Tharp stimulated Alan's interest in botany. Recognizing him as a serious, capable student, each took a personal interest in seeing him succeed. While on sabbatical in Africa, Dr. Turner allowed Alan to stay rent-free in his house and was the first to suggest that he might want to look into the increasingly interesting, relatively new field of palynology. In the fall of 1955, at the beginning of his junior year at UT, Alan began his pollen reference collection, which ultimately grew to 25,000 reference slides of modern flowering plant genera em-

phasizing the Neotropics. The collection was gifted in 2008 to the Smithsonian Tropical Research Institute (STRI), where it is currently being databased in the laboratory of Carlos Jaramillo to be widely available for research. By the time Alan completed his undergraduate degree in 1956, it was clear that paleobotany was the field in which he wanted to specialize.

With Dr. Tharp, Alan spent many weekends traveling to great collecting sites learning the Texas flora and later checking bogs throughout East Texas for a suitable research locality with diverse fossil pollen on which to base his Master's degree. It was also through Professor Tharp's efforts that he obtained support for the M.S. degree from the Humble Oil Company (now part of Exxon Oil), and Dr. Tharp generously donated a car to get to the locality. The M.S. degree was officially directed by Dr. Charles Heimsch, who took Alan as a botany major, while technically the research took place in the geology laboratory of Jane Gray. His first paper, "Pollen analysis of some Texas peat deposits" (Graham & Heimsch, 1960), was based on the Master's degree. It clarified several misconceptions about post-glacial vegetation beyond the glacial boundary—among them, that fir and spruce forests were present in Texas at ca. 9000 years ago and that spruce extended as far south as the Gulf Coast. On reexamining the fossil pollen, he found that fir was not present and that the small quantities of spruce pollen present indicated that spruce had moved southward in the Mississippi Embayment in only limited amounts.

In fall 1958, Alan traveled for the first time to Ann Arbor, Michigan, to start his Ph.D. at the University of Michigan under Chester Arnold, an expert on Paleozoic floras and author of the leading text on paleobotany at that time, *An Introduction to Paleobotany* (Arnold, 1947). At the University, a large collection of macrofossil material from the Sucker and Trout Creek floras of southern Oregon, most of it purchased for the museum from collector Percy Train, provided an opportunity for Alan to study a rich Miocene flora. The initial fossil sorting required a large open space. Arrangements were made for his work in an unheated barn on property at the University of Michigan Botanical Garden, and he survived his first cold Michigan winter of sorting with the aid of a small heater that burned the feet and warmed the knees, but otherwise had little effect on the rest of the surrounding space. Alan credits Estella Leopold at the United States Geological Survey for voluntarily testing some of his material for microfossils early in his study and confirming the abundant presence of fossil pollen in the volcanic shales of the Sucker Creek flora. The results of his dissertation research were thus unusual for that time in treating together both the macrofossils and the microfossils (pollen and spores) of a fossil flora (Graham, 1963). The addition of the microfossils further significantly expanded knowledge of the floral composition. While pursuing the Ph.D., he collaborated on a paper of broader implications, and somewhat unexpected for a paleobotanist, with invertebrate paleontologist Robert V. Kesling, University of Michigan Museum, demonstrating that the classic fossil *Ischadites*, long regarded as occupying a key evolutionary position between the corals and the sponges, was actually a dasycladacean red alga (Kesling & Graham, 1962).

During doctoral studies, in 1960, Alan married Shirley Tousch, a Ph.D. graduate student studying plant taxonomy under Dr. Rogers McVaugh. They spent the first summer of their marriage traveling over 12,000 miles from Michigan throughout Mexico to Chiapas and back, collecting *Cuphea* (Lythraceae) for Shirley's dissertation. Driving an aqua and cream 1952 Chevy sedan bought with a loan from Dr. Tharp, they camped, cooked, and collected for three months, funded by a National Science Foundation grant of $750. They subsequently made numerous other trips to Mexico for collecting and meetings, and during his career at Kent State, Alan spent 12 summers leading a total of about 350 participants on a five-week Kent State University course that he developed entitled "Biological Field Studies in Mexico/Biological Field Studies in the American West." The Grahams have been married for 54 years

and have three children—Andrew, a biostatistician at the University of California, Berkeley in the Department of Vision Science, and father of their granddaughter, Kenzie; Alison, a financial analyst in New York City; and Bruce, a consultant to nonprofit organizations who lives in San Francisco.

After receiving the Ph.D., Alan was a lecturer at the University of Michigan for one year until Shirley completed her degree. A post-doctoral year for both followed at Harvard, for Alan, with paleobotanist Elso Barghoorn and, for Shirley, with taxonomist Carroll Wood. At Harvard, Alan revitalized interest in the classic biogeographic relationship between eastern North America and Eastern Asia with a translation of the 1750 Linnaean dissertation *Plantae Rariores Camschatcenses* (Graham, 1966), and later with publication of *Floristics and Paleofloristics of Asia and Eastern North America*, edited from a symposium organized for the Systematics Section of the XI International Botanical Congress, Seattle, and the Japan–United States Cooperative Science Program, Corvallis (Graham, 1972).

Following Harvard, Alan began a 38-year career (1964–2002) at Kent State University as a Professor of Biological Sciences and Geology, and for the past 12 years has continued as a Research Associate at the Missouri Botanical Garden. While pursuing an active career in research, he remained ever-mindful of the teaching obligations and the responsibilities of university faculty to students. He was particularly sought after for the larger undergraduate biology classes, and he won both the Outstanding Teaching Award from the Student Advisory Council and the Distinguished Scholar Award for Research. Another important activity for that time and place was as Chair of the University Grievance Committee working on behalf of the faculty and as a union negotiator at Kent State for the American Association of University Professors (AAUP).

In the 1960s he initiated an innovative long-term study of tropical American vegetation history with the support of the National Science Foundation that produced a series of publications under the title "Studies in Neotropical Paleobotany" in the *Annals of the Missouri Botanical Garden* and the *American Journal of Botany* (Graham & Jarzen, 1969; Graham, 1976b, 1985, 1988a, 1988b, 1989, 1991a, 1991b, 1991c, 1998, 1999b; Graham et al., 1985, 2000, 2001; Graham & Dilcher, 1998) and an edited symposium volume entitled *Vegetation and Vegetational History of Northern Latin America* organized for the American Institute of Biological Sciences (A.I.B.S.) meetings in Bloomington, Indiana (Graham, 1973). The successful stratagem was to focus initially on lignites and associated sediments that frequently contain plant microfossils and are often well-known geographically and geologically because of their economic importance. The approach ultimately yielded a rich collection of diverse fossil pollen and spores from a variety of locations throughout Latin America ranging in age from the Eocene through the Pliocene. Another edited symposium volume was on the use of non-DNA biological material in forensics for the A.I.B.S. meetings in San Diego (*Forensic Chemistry, Soil Analysis, Entomology, Botany, Palynology, and Other Aspects of Non-Genetic-Marker Biology,* in the *Journal of Forensic Sciences*, Graham, 1997a).

Among the many experiences stimulating Alan Graham's lifelong enthusiasm for teaching and research was an encounter at an evolutionary biology conference in Punta Cana, Dominican Republic. The attendees were invited to a reception hosted by a prominent resident of the island. Alan tells the story that "As I was walking up the grounds of the estate toward the house, someone behind me asked, 'So what are fossils?' I had the pleasure of spending the next enjoyable moments explaining fossils to Oscar de La Renta, one of the genuine, highly successful people in the area of fashion design."

A hallmark of Alan Graham's research has been the integration of paleobotanical data with a broad spectrum of geologic, climatic, and modern floristic and faunal information to form a broad synthesis of New World ecosystems, lineages, and biogeographic history. These summaries are presented in the

books *Late Cretaceous and Cenozoic History of North American Vegetation* (Graham, 1999a; "surely destined to become a classic in its field," from a review in *Taxon*, Cranfill, 2000), *Late Cretaceous and Cenozoic History of Latin American Vegetation and Terrestrial Environments* (Graham, 2010a), and *A Natural History of the New World: The Ecology and Evolution of Plants in the Americas* (Graham, 2010b). Among the paradigm shifts to which his work has contributed was the early demonstration that, in regions where lowland Neotropical rainforest is dominant today, it was not present in the relatively recent geologic past (Graham, 1976a). Prior to that study, it was widely believed that tropical vegetation and climates had extended without interruption from a very remote geologic period, with all of the evolutionary environmental and conservation implications of that misconception. Other contributions have presented the effects of the Early Eocene temperature rise on Neotropical terrestrial vegetation (Graham, 1994); evidence for the recent rise of the high Andes (Graham et al., 2001); and important conceptual articles on Neotropical plant dynamics, geohistory models, and deep-time floras (Graham, 1997b, 2003a, 2003b). He has sought, from among the various disciplines, to bring consistency to studies of New World vegetation and environmental history. His work has lessened the barriers between modern New World ecosystems and the continuum of past events and processes that shaped their origins and distributions. In doing so, he has drawn upon extant communities to interpret the ancient assemblages and has consistently used the latter to better understand how the modern vegetation came to be. In 2009, he was presented both the Asa Gray Award from the American Society of Plant Taxonomists and the Botanical Society of America Merit Award in recognition of his contributions and long-term dedication to botany. In 2011 he was given the Botanical Society of America Paleobotanical Section Award for his outstanding scholarship and contributions to the field. In his 80th year he continues to contribute actively at the Missouri Botanical Garden with his expertise and experienced understanding of the history of New World vegetation and has recently summarized his life and assessed his more than half century of experiences in academics in a forthcoming book, *Academic Tapestries: Fashioning Teachers and Researchers out of Events and Experiences*, published by Missouri Botanical Garden Press.

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RESPONSE OF PLANT DIVERSITY TO MIOCENE FORCING EVENTS: THE CASE OF PATAGONIA

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ABSTRACT

Humid forested communities from eastern Patagonia were replaced by open habitat ecosystems sometime during the mid-Miocene. This major turnover involved a significant physiognomic replacement (i.e., a tree-dominated biome by a shrub-dominated biome), although its associated shift in plant diversity through this time interval has never been quantitatively surveyed. Here, we explore for the first time the diversity patterns of the Miocene spore-pollen records from southern South America. Quantitative results reveal significant differences in the abundance and particularly in the diversity of the major plant groups from the Early to the Late Miocene. Early Miocene spore-pollen assemblages indicate a highly diverse forested ecosystem (rarefied richness at 200 specimens: 64) dominated by podocarps, araucarians, southern beeches, and ferns, with patches of open-habitat species. By the Late Miocene, this was followed by a markedly different community of lower diversity (rarefied richness at 200 specimens: 22) dominated by arid-adapted shrubs of amaranths and *Ephedra*. Ferns and conifers were the most affected groups. Angiosperms slightly declined in diversity yet became dominant for the first time in the Miocene, probably because of their evolutionary adaptability to disturbed habitats, which may have been, in part, responsible for the success of angiosperms overall.

Key words: Miocene, plant diversity, southern South America.

Estimating how diversity of life has fluctuated over geological time is one of the most important goals of paleontology and is crucial for our understanding of recent biotic trends. The analysis of fossil spore-pollen records has proved to be one of the most powerful approaches for quantifying diversity in terrestrial ecosystems (e.g., Jaramillo et al., 2006). The most rigorous tests employed for quantifying diversity using fossil spore-pollen data generally take into account the sampling bias (different sample sizes or density of sampling) and the facies effect (different paleo-environments). Both artifacts can potentially generate patterns in the fossil record that appear to reveal biologically significant phenomena where, in fact, none exist (Signor & Lipps, 1982). In order to avoid these

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effects, a variety of statistical approaches have been applied to compare and estimate species richness from fossil spore- and pollen-bearing samples (Jaramillo & Dilcher, 2000; Jaramillo, 2002; Jaramillo et al., 2010; among others). Despite the recent interest, however, the success of these tools has not yet been evaluated for fossil spore-pollen assemblages preserved in southern South America. Until now, most of the analyses have been limited to counts of numbers of taxa per sample from Patagonian deposits, which have been very useful for revealing qualitatively the major compositional trends (Barreda & Palazzesi, 2007; Palazzesi & Barreda, 2007), although they may fail to identify diversity peaks or declines, particularly when sample size or facies differences have not been adjusted. In this study we quantitatively explore the patterns of diversity of the Miocene spore-pollen records from deposits exposed at eastern Chubut and Santa Cruz provinces, Argentina. It was during the Miocene epoch when one of the most dramatic floristic replacements occurred: the southern beech and podocarp forests that characterized much of the Cenozoic landscapes from eastern Patagonia collapsed by the mid-Miocene and gave rise to a more open vegetation, dominated by arid and semiarid forms (Palazzesi & Barreda, 2012). This major turnover may have led to several extinctions that resulted in relatively low diversity in Late Miocene, although this hypothesis has never been empirically tested. We test this hypothesis and, further, investigate whether or not the resulting patterns of diversity are related to the most important regional (e.g., Andean uplift) and global (e.g., Antarctic ice sheets) events in the Miocene in southern South America.

MATERIALS AND METHODS

GEOLOGICAL SETTING, SAMPLING, AND ANALYSIS

Detailed palynological analyses of the Chenque and Puerto Madryn formations were undertaken for the diversity analysis of the Miocene paleoflora from eastern Patagonia (Fig. 1). The Early Miocene is represented by three sampled sections: Cerro Chenque (208 m), Cerro Viteau (117 m), and Cañadón Baumann (64 m); the Late Miocene by two sections: Puerto Pirámides (15 m) and Punta Pardelas (10 m). These sections consist mainly of fine-grained sandstones, coquinas, and

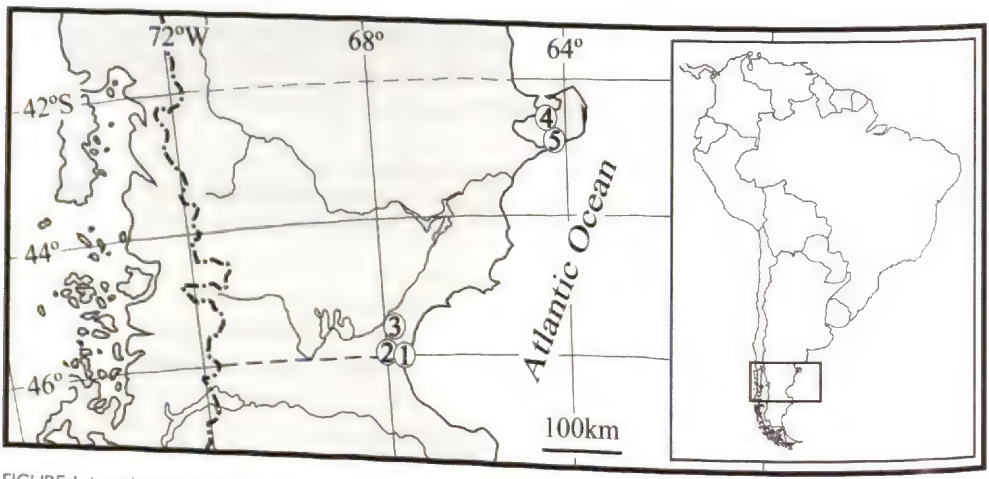

FIGURE 1. Location map of sampled sections. (1) Cerro Chenque (45.941106°S, 67.569012°W); (2) Cerro Viteau (45.831475°S, 67.470632°W); (3) Cañadón Baumann (45.743927°S, 67.865335°W); (4) Puerto Pirámides (42.574850°S, 64.304600°W); (5) Punta Pardelas (42.618768°S, 64.257544°W).

heterolithic beds. The geological setting, stratigraphy, depositional environment, and age constraints of the sampling units have been analyzed in detail elsewhere (Barreda, 1996; Palazzesi & Barreda, 2004). We performed quantitative and taxonomic palynological analyses on a total of 40 samples, from which we selected 23 accumulated in marine environments during times of mid-highstand. These selected samples contain marine and continental palynomorphs.

Standard palynological techniques were used to process all samples (Traverse, 2007). A minimum of 200 continental specimens were counted in each sample, for a total of 7962 counted specimens. All slides and residues are housed at the palynotheca of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia."

QUANTITATIVE ANALYSIS

All quantitative analyses were done using the R software program, version 2.2.0 (R Development Core Team, 2007). We arranged pollen data in a sample by taxon matrix (not shown here due to space limitation) in which each cell contained the raw data of each taxon per sample. This matrix was subjected to a number of techniques to explore (1) sample and species association and (2) species diversity.

Sample and species association. We conducted a constrained cluster analysis to explore sample associations (Q-mode). For this purpose, we used the "chclust" function of the R program's package "rioja" (Juggins, 2012), which performs a constrained cluster analysis of a distance matrix with clusters constrained by sample order. The distance matrix used was the Bray-Curtis metric (Bray & Curtis, 1957), and the agglomeration method was the coniss (Juggins, 2012). As opposed to unconstrained cluster analyses, only stratigraphically adjacent clusters are considered for merging. This method has been widely used and has proven to be particularly satisfactory for pollen frequency data (Grimm, 1987). The resulting groups of samples were used as the main sampling units for subsequent analyses (among-sample diversity). The NMDS is regarded as the most robust unconstrained ordination method in community ecology (Minchin, 1987), and aims at plotting dissimilar objects far apart in the ordination space and similar objects close to one another. We ordinated the samples (along with the species) using the "metaMDS" function of the R's package "vegan" (Oksanen et al., 2012), computed using the Bray-Curtis distance metric (Bray & Curtis, 1957). All analyses were run on square root transformation, which partially reduces the problems associated with closed sum percentage data, improves normality, and is highly recommended when using count variables (Sokal & Rohlf, 1995).

Species diversity. Patterns in diversity can be obtained by exploring the variation in the number of species (richness) and whether these species are evenly distributed or dominated by a minority (evenness). We calculated richness by means of rarefaction, the Shannon-Wiener index, the Simpson index, evenness, standing diversity, and bootstrapped species accumulation curves. The first three indices are very closely related (Hill, 1973). Rarefaction allows us to calculate species richness for a given number of individual samples, based on the construction of rarefaction curves. These curves are created by randomly resampling the pool of samples multiple times and then plotting the average number of species found in each sample (Sanders, 1968). We rarified all the samples to a common count level of 200 specimens and performed comparisons for the Early Miocene and Late Miocene assemblages. For comparison purposes, we also used rarefied pollen counts from one Pleistocene palynological assemblage. Differences in rarified species richness were determined among the Early Miocene and the Late Miocene assemblages using ANOVA tests and post hoc Tukey tests. The Shannon-Wiener index is species abundance and species richness dependent, sensitive to changes

in the importance of the rare species (Solow, 1993) and one of the most commonly used indices (Kent, 2012). The Simpson index considers the probability that two randomly chosen individuals from a given sample are different species, so it emphasizes common species over rare ones. Evenness led us to infer how the relative abundance is distributed among species (Huston, 1994). It is simply a measure of how similar species are in their abundances and ranges from zero when most individuals belong to a few species, to one, when species are nearly equally abundant (Smith & Wilson, 1996). The range-through method was used to estimate standing diversity. This method assumes that a taxon is present in a sample if it is found both above and below it (Jaramillo & Dilcher, 2000; Jaramillo, 2008), and so it tends to minimize facies effect. Taxa that are present in only one sample were excluded for this analysis, because they can introduce noise into the diversity pattern (Wing, 1998). Standing diversity richness (total) and for each main botanical group (ferns, gymnosperms, and angiosperms) were calculated among the Early Miocene and the Late Miocene samples. Finally, we calculated the bootstrapped species accumulation curves using the R program's "specaccum" function (package "vegan") for comparison of diversity among groups of samples for all species in the assemblages, according to the method of Willot (2001). This tests if the rate of species accumulation differed among the constrained groups defined by the cluster analysis.

RESULTS

PLANT COMPOSITION

One hundred fifty fossil pollen and spore types were identified from Miocene deposits of eastern Patagonia and assigned to formally described fossil genera or species (Table 1). Fossil spores or pollen of selected species are illustrated in Figure 2. Cluster analysis (Q-mode) revealed two stratigraphically well-ordered major groups of samples with rather different spore-pollen composition (Fig. 3): Group A comprises the Early Miocene samples (EM1–EM18), with two subgroups, A1 (samples EM1–EM13) and A2 (samples EM14–EM18). Group B comprises all Late Miocene samples (samples ET19–ET23). Group A (Early Miocene) is dominated by conifers (about 40%), followed by southern beeches (about 20%) and fern spores (about 15%). Conifers are largely represented by podocarps (*Podocarpus* L'Hér. ex Pers., *Dacrydium* Lamb., *Lagarostrobos* Quinn, *Dacrycarpus* (Endl.) de Laub., *Saxegothaea* Lindl., and *Microcachrys* Hook. f. types) and araucarians (*Araucaria* Juss.). Cupressaceae is scarce; other gymnosperms (Ephedraceae) occur at lower abundances (Tables 1, 2). Southern beeches (Nothofagaceae) are fairly diverse, with the four extant subgroups recorded and *Nothofagus* Blume subg. *Nothofagus* being the most abundant. Other well-represented angiosperms include Amaranthaceae and Arecaceae. There are also records of other monocots (mainly aquatic herbs of Cyperaceae and Typhaceae) and diverse dicots (Asteraceae, Malvaceae [Bombacoideae], Chloranthaceae, Onagraceae, Proteaceae, among others). Ferns are represented mainly by Dicksoniaceae (*Lophosoria* C. Presl), Cyatheaceae (*Cyathea* Sm.), and Blechnaceae.

Subgroup A1 is divided into two minor groups, A1a and A1b (Tables 1, 2, Fig. 3), that are distinct from one another and from subgroup A2 mainly on the basis of the presence of stratigraphically important species (e.g., *Glencopollis ornatus* Pocknall & Mildenhall 1984, *Tubulifloridites antipodica* Cookson 1974, *Baumannipollis chubutensis* Barreda 1993) and the abundance of some plant lineages. For example, palm pollen is abundant in subgroup A1a, reaching its maximum in sample EM4 (13%), then, although present throughout all Early Miocene samples, there is a broad decline in abundance toward the levels containing subgroups A1b and A2. A similar general trend is observed in Araucariaceae and Ephedraceae. In the upper part of subgroup A1a, some warm-loving taxa are recorded (e.g., Malvaceae

TABLE 1. Left column lists fossil taxa from the Chenque and Puerto Madryn formations, based on previously published data (Barreda, 1996, 1997a–1997d; Barreda & Palamarczuk, 2000; Palazzesi & Barreda, 2004; Barreda et al., 2008a, 2008b, 2010; Palazzesi et al., 2009, 2010) and unpublished new information; right column lists botanical affinities.

Fossil taxon	Nearest living relatives
Bryophyte spores	
Coptospora archangelskyii Zamaloa 2004	Bartramiaceae
cf. *Riella*	Riellaceae (*Riella* Mont.)
Stereisporites antiquasporis (Wilson & Webster) Dettmann 1963	Sphagnaceae
Stereisporites sp.	Sphagnaceae
Lycophyte spores	
Foveotriletes sp.	Lycopodiaceae (*Lycopodium* L.)
Retitriletes austroclavatidites (Cooks.) Dör. Kr. Mai & Schulz 1963	Lycopodiaceae (*Lycopodium*)
Pteridophyte spores	
Azolla sp.	Azollaceae (*Azolla* Lam.)
Baculatisporites comaumensis (Cookson) Potonié 1953	Hymenophyllaceae? Osmundaceae
Baculatisporites disconformis Stover 1973	Hymenophyllaceae? Osmundaceae
Biretisporites crassilabratus Archangelsky 1972	unknown fern
Cyatheacidites annulatus Cookson 1947	Dicksoniaceae (*Lophosoria quadripinnata* (J. F. Gmel.) C. Chr.)
Cyathidites australis Couper 1953	Cyatheaceae (*Cyathea*)
Cyathidites minor Couper 1953	unknown fern
Cyathidites paleospora (Martin) Alley & Broadbridge 1992	Cyatheaceae (*Cyathea*)
Cyathidites patagonicus Archangelsky 1972	unknown fern
Cyathidites subtilis Stover & Partridge 1973	Cyatheaceae (*Cyathea*)
Deltoidospora sp.	unknown fern
Echinosporis sp.	unknown fern
Gleicheniidites circinidites (Cookson) Dettmann 1963	Gleicheniaceae
Granulatisporites sp.	unknown fern
Ischyosporites areapunctatis (Stuchlik) Barreda 1997	Dicksoniaceae
Laevigatosporites ovatus Wilson & Webster 1946	Blechnaceae
Leiotriletes cf. *regularis* (Pflug) Krutzsch	unknown fern
Matonisporites ornamentalis (Cookson) Partridge 1973	Dicksoniaceae (*Dicksonia* L'Hér.)
Matonisporites sp.	Dicksoniaceae
Monolites sp.	Polypodiaceae
Muricingulisporis chenquensis Barreda 1992	Pteridaceae (*Pteris semiadnata* Phil.)
Peromonolites vellosus Partridge 1973	Blechnaceae?
Polypodiisporites cf. *minimus* (Coup) Kh. & Mart. emend. Pock. & Mild 1984	Polypodiaceae
Polypodiisporites inangahuensis (Coup) Pot. emend. Pock. & Mild. 1984	Polypodiaceae
Polypodiisporites radiatus Pocknall & Mildenhall 1984	Polypodiaceae
Reticuloidosporites tenellis Krutzsch 1959	Polypodiaceae
Trilites parvallatus Krutzsch 1959	Dicksoniaceae
Trilites sp.	unknown fern
Trilites tuberculiformis Cookson 1947	Dicksoniaceae
Verrucosisporites kopukuensis (Couper) Stover 1973	Schizaeaceae (*Lygodium* Sw.)

(*continued*)

TABLE 1. (*continued*)

Fossil taxon	Nearest living relatives
Gymnosperm pollen	
Araucariacites australis Cookson 1947	Araucariaceae (*Araucaria*)
Dacrycarpites australiensis Cookson & Pike 1953	Podocarpaceae (*Dacrycarpus*)
Equisetosporites claricristatus (Shakmundes) Barreda 1997	Ephedraceae (*Ephedra*)
Equisetosporites lusaticus (Shakmundes) Barreda	Ephedraceae (*Ephedra*)
Equisetosporites notensis (Cookson) Romero 1977	Ephedraceae (*Ephedra*)
Gamerroites cf. *psilasaccus* (Archangelsky & Romero) Archangelsky 1988	Podocarpaceae
Inaperturopollenites sp. 1	Cupresaceae (*Pilgerodendron* Florin type)
Inaperturopollenites sp. 2	Podocarpaceae (*Saxegothaea* type)
Lygistepollenites florinii (Cookson & Pike) Stover & Evans 1973	Podocarpaceae (*Dacrydium*)
Microcachrydites antarcticus Cookson 1947	Podocarpaceae (*Microcachrys*)
Phyllocladidites mawsonii Cookson 1947	Podocarpaceae (*Lagarostrobos*)
Podocarpidites cf. *exiguus* Harris 1965	Podocarpaceae (*Podocarpus*)
Podocarpidites elegans Romero 1977	Podocarpaceae (*Podocarpus*)
Podocarpidites ellipticus Cookson 1947	Podocarpaceae (*Podocarpus*)
Podocarpidites marwickii Couper 1953	Podocarpaceae (*Podocarpus*)
Podocarpidites microreticuloidata Cookson 1947	Podocarpaceae (*Podocarpus*)
Podocarpidites rugulosus Romero 1977	Podocarpaceae (*Podocarpus*)
Trisaccites microsaccatum Couper 1953	extinct Podocarpaceae
Angiosperm pollen	
Acaciapollenites myriosporites (Cookson) Mildenhall 1972	Fabaceae Mimosoideae (*Acacia* Mill.)
Arecipites otagoensis (Couper) Mildenhall & Pocknall 1989	Arecaceae
Arecipites subverrucatus (Pocknall) Mildenhall & Pocknall 1989	Arecaceae
Arecipites sp. 1	Arecaceae
cf. *Bauhinia*	Fabaceae (Caesalpinioideae) (*Bauhinia* L.)
Baumannipollis chubutensis Barreda 1993	Malvaceae
Baumannipollis variaperturatus Barreda 1993	Malvaceae
Canthiumidites bellus (Stover & Partridge) Mildenhall & Pocknall 1989	Rubiaceae
Chenopodipollis chenopodiaceoides (Martin) Truswell et al. 1985	Amaranthaceae
Clavatipollenites sp.	Chloranthaceae
Corsinipollenites atlantica Barreda 1997	Onagraceae
Cupanieidites reticularis Cookson & Pike 1954	Sapindaceae (Cupanieae)
Cyperaceaepollis neogenicus Krutzsch 1970	Cyperaceae
Diporites aspis Pocknall & Mildenhall 1984	Onagraceae (*Fuchsia* L.)
Dryadopollis minima Barreda 1997	Salicaceae?
Ericipites sp.	Ericaceae/Epacridaceae
Glencopollis ornatus Pocknall & Mildenhall 1984	Polygonaceae (*Polygonum* L.)
Gothanipollis sp.	Loranthaceae
Graminidites sp.	Poaceae
Granodiporites nebulosus Stover & Partridge 1973	Proteaceae (*Embothrium coccineum* J. R. Forst.& G. Forst.)
Haloragacidites myriophylloides Cookson & Pike 1954	Haloragaceae (*Myriophyllum* L.)
Haloragacidites trioratus Couper 1953	Casuarinaceae
Huanilipollis cabrerae Barreda & Palazzesi 2008	Asteraceae (Nassauviae) (*Holocheilus* Cass. type)

TABLE 1. (*continued*)

Fossil taxon	Nearest living relatives
Huanilipollis criscii Barreda & Palazzesi 2008	Asteraceae (Nassauviae) (*Triptilion* Ruiz & Pav. type)
Ilexpollenites sp.	Aquifoliaceae (*Ilex*)
Intratriporopollenites sp.	Malvaceae (Bombacoideae)
Liliacidites sp. 1	Bromeliaceae?
Liliacidites sp. 2	Liliaceae
Liliacidites sp. 3	Juncaceae?
Malvacipolloides comodoroensis Barreda 1993	Malvaceae
Margocolporites tenuireticulatus Barreda 1997	Fabaceae (*Prosopis* type)
Margocolporites vanwijhei Germeraad et al. 1968	Fabaceae (Caesalpinoideae)
Margocoporites sp. 1	Fabaceae (*Prosopis*)
Milfordia argentina Barreda 1997	Sparganiaceae?
Mutisiapollis patersonii Macphail & Hill 1994	Asteraceae (Mutisieae) (*Mutisia* L. f. type)
Mutisiapollis viteauensis (Barreda) Barreda 1997	Asteraceae (Mutisieae) (*Cnicothamnus* Grisib. type)
Myrtaceidites sp.	Myrtaceae
Myrtaceidites verrucosus Partridge 1973	Myrtaceae
Nothofagidites acromegacanthus Menéndez & Caccavari 1975	*Nothofagus* (*Fuscospora* (R. S. Hill & J. Read) Heenan & Smissen?)
Nothofagidites americanus Zamaloa 1992	*Nothofagus* (*Lophozonia* Turcz.)
Nothofagidites dorotensis Romero 1973	*Nothofagus* (*Brassospora* Philipson & Philipson)
Nothofagidites flemingii (Cookson) Potonié 1960	*Nothofagus* (*Nothofagus*)
Nothofagidites saraensis Menéndez & Caccavari 1975	*Nothofagus* (*Nothofagus*)
Nothofagidites tehuelchesii Zamaloa & Barreda 1992	*Nothofagus* (*Lophozonia*)
Nyssapollenites endobalteus (Mc Int.) Kemp & H. emend. Mild. & Pock.1989	unknown
Orapollis sp. 1	Vivianiaceae (*Rhynchotheca* Ruiz & Pav. type)
Orapollis sp. 2	Vivianiaceae (*Balbisia* Cav. type)
Orapollis sp. 3	Vivianiaceae (*Viviania* Cav. type)
Perforotricolpites sp.	Convolvulaceae
Periporopollenites vivianae Mautino 2011	Cactaceae (*Opuntia* Mill.)
Perisyncolporites pokornyi Germeraad et al. 1968	Malpighiaceae
Poluspissusites puntensis Barreda 1997	Goodeniaceae
Polyadopollenites sp.	Fabaceae (*Anadenanthera* Speg.)
Polycolpopollenites sp.	unknown
Polycolporopollenites sp.	Rosaceae?
Proteacidites obscurus Cookson 1950	Proteaceae
Proteacidites pseudomoides Stover 1973	Proteaceae (*Lomatia* R. Br. type)
Proteacidites sp. 1	Proteaceae (*Orites* R. Br. type)
Pseudowintherapollis couperi Krutzsch emend. Mildenhall 1979	Winteraceae (*Drimys winteri* J. R. Forst & G. Forst)
Psilatricolpites sp.	unknown
Psilatricolporites operculatus Van der Hammen & Wymstra 1964	Euphorbiaceae (*Alchornea* Sw.)
Psilatricolporites protrudens Palazzesi & Barreda 2010	Calyceraceae
Psilatricolporites quenua Barreda & Palazzesi 2009	Rosaceae (*Polylepis* Ruiz & Pav./*Acaena* Mutis ex L.)
Psilatricolporites sp.	Rosaceae

(*continued*)

TABLE 1. (*continued*)

Fossil taxon	Nearest living relatives
Quilembaypollis gamerroi Palazzesi & Barreda 2009	Asteraceae (Barnadesioideae) (*Chuquiraga*)
Quilembaypollis stuessyi Palazzesi & Barreda 2009	Asteraceae (Barnadesioidea) (*Schlechtendalia* Less.)
Quilembaypollis tayuoides Barreda & Palazzesi 2009	Asteraceae (Barnadesioidea) (*Dasyphyllum* Kunth)
Quintiniapollis striatulosa Barreda 1997	Paracryphiaceae (*Quintinia* A. DC.)
Retitricolporites cienaguensis Dueñas 1980	Euphorbiaceae?
Retitricolporites romeroi (Baldoni) Barreda 1997	unknown
Rhoipites baculatus Archangelsky 1973	unknown
Rhoipites minusculus Archangelsky 1973	unknown
Rhoipites sp. 1	Celastraceae (*Maytenus* Molina type)
Rhoipites sp. 2	unknown
Rhoipites sp. 3	unknown
Rhoipites sp. 4	unknown
Rhoipites sp. 5	unknown
Rubipollis oblatus (Pocknall & Mildenhall) Mildenhall & Pocknall 1989	Rubiaceae (*Canthium* Lam.)
Senipites patagonica Barreda 1997	Symplocaceae (*Symplocos*)
Sparganiaceaepollenites barungensis Harris 1972	Sparganiaceae/Thyphaceae
Sparganiaceaepollenites sp. 1	Sparganiaceae/Thyphaceae
Sparsipollis sp.	unknown
Striatricolporites gamerroi Archangelsky 1973	Anacardiaceae
Striatricolporites sp.	Anacardiaceae (*Schinus*)
Thymelaepollis sp.	Thymelaeaceae (*Ovidia* Meisn.)
Tricolpites reticulatus Cookson 1947	Gunneraceae (*Gunnera* L.)
Tricolpites trioblatus Mildenhall & Pocknall 1989	Convolvulaceae (*Cressa* L./*Wilsonia* R. Br.)
Tricolpites sp. 1	unknown
Tricolpites sp. 2	unknown
Tricolpites sp. 3	unknown
Tricolpites sp. 4	unknown
Triporopollenites minor (Couper) Barreda 1993	unknown
Triporopollenites sp.	Proteaceae?
Tubuliflordites antipodica Cookson 1974	Asteraceae
Tubuliflordites pleistocenicus Martin 1973	Asteraceae
Tubuliflordites simplis Martin 1973	Asteraceae

[Bombacoideae], Sapindaceae [*Cupania* L.], Aquifoliaceae [*Ilex* L.]). Group B (Late Miocene) is dominated by amaranth, Ephedraceae, and aquatic monocots (Cyperaceae, Typhaceae). Conifers (podocarps, araucarians), southern beeches (Nothofagaceae), and ferns are scarce (Fig. 3). Asteraceae, on the contrary, increase in both abundance and diversity.

NMDS analysis (Q-mode) supports the clustering of samples defined above, clearly separating the Early Miocene samples (EM1–EM18) from those of the Late Miocene (LM19–LM23, Fig. 4). NMDS analysis (R-mode) leads to the recognition of two major groups of species that tend to co-occur. Group 1 is composed of conifers, southern beeches, palms, and ferns; Group 2 is composed of

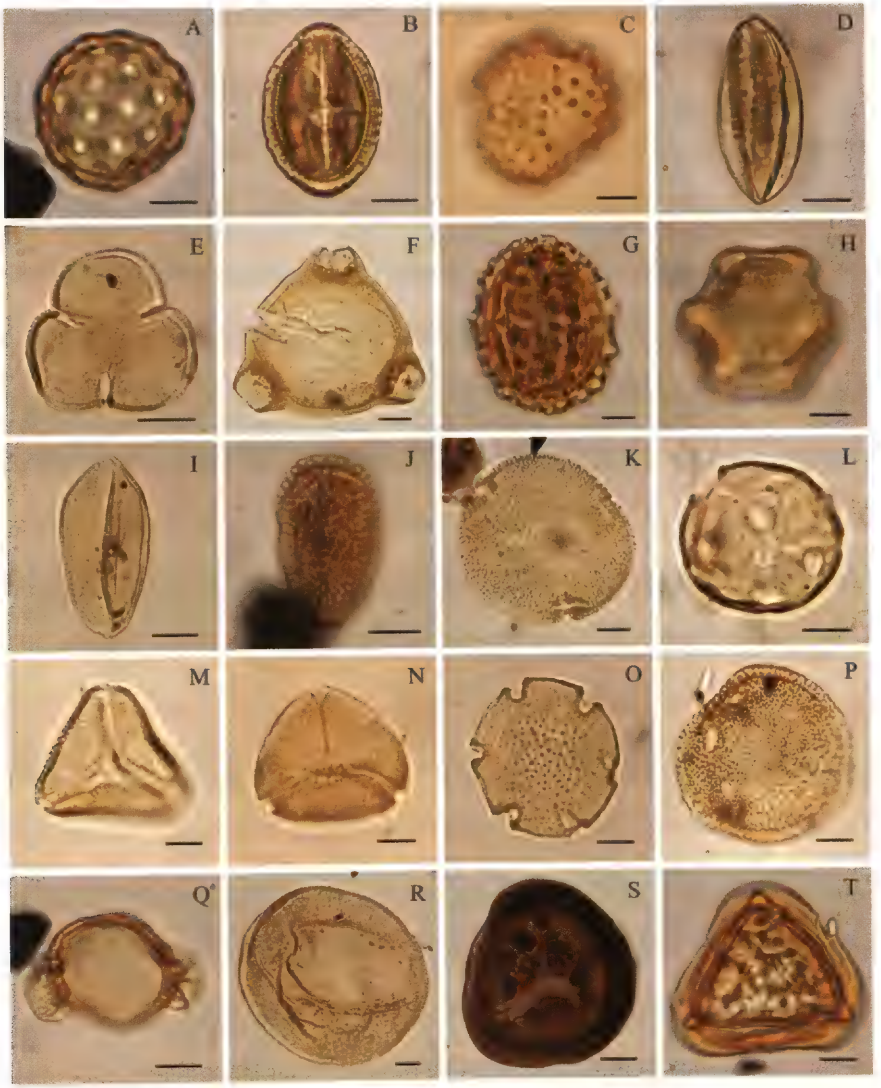

FIGURE 2. Spores and pollen from selected characteristic species from Late (A–D) and Early Miocene (E–T) Puerto Madryn and Chenque formations, respectively. —A. *Chenopodipollis chenopodiaceoides* BAPal 6011b: N49/3. —B. *Mutisiapollis patersonii* BAPal 6011b: X38/1. —C. *Tubuliflordites pleistocenicus* BAPal 6011b: L51/4. —D. *Equisetosporites claricristatus* BAPal 6011b:R32/3. —E. *Tricolpites reticulates* BAPal ex CIRGEO Palin 881: U55/3. —F. *Corsinipollenites atlantica* BAPal ex CIRGEO Palin 958: W47/3. —G. *Mutisiapollis viteauensis* BAPal ex CIRGEO Palin 844: U47/3. —H. *Quilembaypollis tayuoides* BAPal ex CIRGEO Palin 847: N45/1. —I. *Arecipites subverrucatus* BAPal ex CIRGEO Palin 847: H35/2. —J. *Ilexpollenites* sp. BAPal ex CIRGEO Palin 854: U46/3. —K. *Intratriporopollenites* sp. BAPal ex CIRGEO Palin 959: Q41. —L. *Perisyncolporites pokornyi* BAPal ex CIRGEO Palin 959: W52/2. —M. *Cupanieidites reticularis* BAPal ex CIRGEO Palin 957: V30/4. —N. *Myrtaceidites verrucosus* BAPal ex CIRGEO Palin 855: V34/4. —O. *Nothofagidites acromegacanthus* BAPal ex CIRGEO Palin 845: M51. —P. *Thymelaepollis* sp. BAPal ex CIRGEO Palin 949: K35/1. —Q. *Phyllocladidites mawsonii* BAPal ex CIRGEO Palin 845: O47/4. —R. *Araucariacites australis* BAPal ex CIRGEO Palin 956: Q48. —S. *Cyatheacidites annulatus* BAPal ex CIRGEO Palin 842: R48. —T. *Muricingulisporis chenquensis* BAPal ex CIRGEO Palin 844: W36. Scale bars equal 10 µm, except in parts A, C, G, H, K, M, N, and O, where scale bars equal 5 µm. Authorities are given in Table 1. Coordinates of the illustrated specimens refer to the England slide finder grid (PYSER-SGI Limited, Kent, United Kingdom).

TABLE 2. Species list and proportional abundances. See Table 1 for full names and authorities of taxa.

	Relative frequencies									
Fossil taxa	**EM1**	**EM2**	**EM3**	**EM4**	**EM5**	**EM6**	**EM7**	**EM8**	**EM9**	**EM10**
Bryophyte spores										
C. archangelskyi	0.23	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cf. *Riella*	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. antiquasinus	0.00	0.27	0.22	0.22	0.39	0.00	0.35	0.00	0.00	0.00
Stereisporites sp.	0.00	0.00	0.22	0.90	0.00	0.40	0.00	0.00	0.00	0.00
Lycophyte spores										
Foveotriletes sp.	0.23	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. australiensiformis	0.00	0.27	0.22	0.22	0.39	0.00	0.00	0.00	0.00	0.43
Pteridophyte spores										
Azolla sp.	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.34	0.00	0.00
B. comaumensis	0.46	0.55	0.00	0.45	0.00	0.00	0.35	0.00	0.00	0.43
B. dissectiformis	0.23	0.27	0.67	0.00	0.39	0.40	1.05	0.34	0.41	0.85
B. crassilabratus	0.23	0.55	0.22	0.22	0.39	0.00	0.00	0.34	0.41	0.43
C. annulatus	1.37	1.65	1.11	1.80	0.79	0.40	1.39	2.39	1.24	0.85
C. australis	2.29	1.92	1.11	3.37	0.79	0.40	1.39	0.34	0.00	2.14
C. minor	0.46	1.37	0.22	0.22	0.39	0.79	0.35	0.00	0.00	1.28
C. paleospora	0.00	0.00	0.00	0.00	0.39	1.19	0.70	0.00	0.00	0.00
C. patagonicus	0.92	0.27	0.44	0.67	0.00	0.40	0.00	0.00	0.00	0.00
C. subtilis	0.00	0.55	0.89	2.02	0.00	0.00	0.00	0.00	0.00	0.00
Deltoidospora sp.	0.23	0.55	0.22	0.22	0.39	0.40	0.35	0.34	1.24	0.43
Echinosporis sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43
G. circumcites	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.34	0.41	0.43
Granulatisporites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00
I. areapunctatis	0.23	0.55	0.22	1.12	0.39	0.40	0.70	1.02	0.00	0.85
L. ovatus	1.37	3.02	1.77	2.25	2.76	3.56	4.53	1.02	0.83	2.99
L. regulatus	0.46	0.27	0.44	2.02	0.39	1.58	0.35	1.37	0.41	0.43
M. ornamentalis	0.23	0.27	0.22	0.00	0.00	0.00	0.00	0.00	0.41	0.00
Matonisporites sp.	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Monolites sp.	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.00	0.00
M. chenquensis	0.00	0.00	0.44	0.00	0.39	0.00	0.00	0.00	0.00	0.43
P. vellosus	0.23	0.27	0.00	0.22	0.00	0.40	0.00	0.34	0.00	0.43
P. cf. minimus	0.00	0.27	0.00	0.22	0.00	0.00	0.35	0.00	0.00	0.00
P. mangahuensis	0.23	0.27	0.22	0.22	0.00	0.00	0.00	0.34	0.41	0.43
P. radiatus	0.23	0.27	0.44	0.00	0.00	0.00	0.35	0.00	0.00	0.43
R. tenellis	0.46	0.27	0.00	0.22	0.00	0.40	0.35	0.00	0.41	0.43
T. parvithelatus	0.23	0.27	0.22	0.00	0.00	0.40	0.35	0.00	0.00	0.43
Trilites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. tuberculiformis	0.23	0.27	0.22	0.67	0.00	0.40	0.00	0.00	0.41	0.43
V. kopukuensis	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gymnosperm pollen										
A. australis	26.77	10.99	13.75	6.74	6.69	7.11	7.32	12.63	11.20	1.71
D. australiensis	0.46	0.27	0.44	0.22	0.39	0.00	0.35	0.00	0.41	0.85

EM11	EM12	EM13	EM14	EM15	EM16	EM17	EM18	LM19	LM20	LM21	LM22	LM23
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.49
0.44	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.00	0.21	0.25	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.00	0.74	0.63	0.25	0.40	0.46	0.00	0.00	0.00	0.35	1.46
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.49	0.21	0.50	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.21	0.25	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.88	4.18	0.46	0.98	1.47	1.00	1.20	1.84	0.00	0.00	0.00	0.00	0.00
1.32	0.98	0.00	0.49	2.31	2.25	0.80	0.61	0.00	0.00	0.00	0.00	0.00
0.88	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.88	0.25	0.00	5.64	3.14	4.00	4.42	5.36	6.69	3.80	7.29	5.54	4.39
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.88	0.25	0.00	0.25	0.21	0.50	0.40	0.15	0.00	0.00	0.00	0.00	0.00
1.76	1.47	1.38	1.96	0.42	0.50	2.41	2.45	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	1.72	1.68	2.75	1.61	1.53	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.49	0.21	0.25	0.40	0.77	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.25	0.21	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.00	0.21	0.00	0.40	0.15	2.09	1.90	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.21	0.25	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.21	0.25	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4.41	3.44	1.83	2.70	6.50	2.00	7.23	2.91	0.00	0.76	1.04	1.38	0.49
0.44	1.23	0.46	0.25	0.21	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00

(continued)

TABLE 2. (*continued*)

	Relative frequencies									
Fossil taxa	**EM1**	**EM2**	**EM3**	**EM4**	**EM5**	**EM6**	**EM7**	**EM8**	**EM9**	**EM10**
E. daricristatus	3.43	3.85	3.77	4.94	3.54	2.77	3.83	6.48	2.07	0.85
E. lusaticus	0.23	0.27	0.00	0.22	0.79	0.00	0.70	1.02	0.00	0.43
E. notensis	0.00	0.27	0.00	0.45	0.39	0.00	0.00	1.02	2.07	0.43
G. cf. psilasaccus	0.92	1.10	2.22	0.45	0.39	1.19	0.35	0.34	0.83	3.42
I. sp. 1	1.14	0.82	1.11	0.90	2.76	2.77	1.39	0.34	4.98	0.85
I. sp. 2	0.46	0.27	0.67	0.22	0.39	0.40	0.35	0.34	1.24	0.43
L. florinii	0.92	0.27	0.22	1.80	1.18	0.40	0.35	0.34	0.41	2.14
M. antarcticus	0.69	0.27	0.67	0.45	0.79	0.79	0.35	0.00	0.00	0.43
P. mawsonii	0.69	1.37	1.33	0.67	1.57	2.37	2.44	1.37	4.15	5.56
P. cf. exiguus	0.00	0.27	0.67	0.00	0.39	0.40	0.00	0.00	0.00	0.00
P. elegans	2.75	4.67	1.77	5.39	2.76	5.53	3.48	2.73	4.15	8.97
P. ellipticus	8.01	9.34	7.98	4.49	10.63	8.70	1.05	0.34	3.32	3.85
P. marwickii	11.44	10.16	11.97	2.70	10.24	5.14	8.36	18.09	2.90	3.42
P. microreticuloidata	4.81	1.37	0.22	1.57	0.39	1.19	2.09	2.39	1.66	6.84
P. rugulosus	5.03	4.12	7.54	7.19	5.51	3.95	3.14	2.73	3.73	6.41
T. microsaccatum	0.00	0.00	0.22	0.00	0.00	0.40	0.35	0.00	0.00	0.43
Angiosperm pollen										
A. myriosporites	0.00	0.00	0.00	0.00	0.00	0.40	0.35	0.00	0.00	0.00
A. otagoensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02	0.41	0.85
A. subverrucatus	8.01	4.67	2.22	12.81	1.57	5.53	3.14	1.02	0.41	0.43
A. sp. 1	0.00	0.27	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00
cf. *Bauhinia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B. chubutensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B. variaperturatus	0.23	0.27	0.22	0.22	0.39	0.00	0.35	0.34	0.41	0.43
C. bellus	0.23	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00
C. chenopodiaceoides	0.92	2.20	3.10	1.57	6.30	3.16	7.67	2.39	6.64	0.85
Clavatipollenites sp.	0.00	0.00	0.00	0.00	0.00	0.40	0.70	0.00	0.00	0.00
C. atlantica	0.00	0.00	0.22	0.00	0.39	0.00	1.05	0.00	0.00	0.43
C. reticularis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. neogenicus	0.92	0.82	0.44	0.00	0.79	2.37	1.05	1.02	0.00	2.56
D. aspis	0.00	0.27	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00
D. minima	0.23	0.27	0.22	0.22	0.00	0.40	0.35	0.00	0.00	0.00
Ericipites sp.	0.00	0.00	0.00	0.22	0.00	0.00	0.35	0.00	0.83	0.00
G. ornatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.41	0.00
Gothanipollis sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Graminidites sp.	0.92	1.65	1.33	0.45	1.18	3.56	3.48	1.37	0.83	1.28
G. nebulosus	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00
H. myriophylloides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H. trioratus	0.23	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00
H. cabrerae	0.23	0.00	0.44	0.45	0.00	0.00	0.00	0.68	0.00	0.00
H. criscii	0.00	0.00	0.22	0.00	0.00	0.40	0.00	0.00	0.00	0.00
Ilexpollenites sp.	0.00	0.00	0.00	0.00	0.39	0.40	0.35	0.00	0.00	0.00

EM11	EM12	EM13	EM14	EM15	EM16	EM17	EM18	LM19	LM20	LM21	LM22	LM23
0.44	0.25	0.46	0.25	0.21	0.25	0.40	0.00	11.30	13.31	27.78	13.15	4.39
0.44	1.97	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	0.49	0.21	0.25	0.40	0.15	8.37	4.56	2.78	5.19	9.27
0.88	0.74	0.92	1.23	1.89	2.00	3.61	2.45	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	0.25	0.21	0.50	0.40	0.31	0.00	0.00	0.00	0.00	0.00
1.76	1.97	0.00	0.49	0.63	0.50	0.80	0.15	0.00	0.00	0.00	0.00	0.00
0.44	0.98	0.46	0.49	1.68	0.75	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.46	0.25	0.00	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3.52	8.60	4.59	6.13	6.71	8.50	5.22	4.29	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.32	2.95	2.75	2.21	2.10	2.75	2.41	2.76	0.00	0.00	0.00	0.00	0.00
3.52	5.16	13.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2.20	3.69	2.29	4.17	3.77	6.75	7.23	3.98	0.00	0.00	0.00	0.00	0.00
9.25	11.06	1.38	3.19	11.32	10.00	10.04	7.81	0.00	0.00	0.00	0.00	0.00
9.25	7.37	13.76	3.92	3.77	6.00	4.82	1.38	0.84	2.66	3.82	8.65	9.27
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.32	0.74	0.46	1.23	0.42	0.75	0.00	0.31	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.42	0.25	0.80	0.31	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	0.98	0.63	1.75	0.80	0.46	0.42	1.52	0.69	1.38	2.93
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2.20	3.44	0.92	3.43	9.43	0.75	6.43	7.66	36.82	33.84	11.81	20.76	38.54
0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.00	0.25	0.00	0.50	0.00	0.31	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.21	0.00	0.80	0.15	0.00	0.00	0.00	0.00	0.00
2.64	1.23	6.42	6.13	5.66	4.25	5.62	7.81	3.77	0.38	9.03	6.23	2.93
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.25	0.00	0.00	0.00	0.46	0.00	0.00	0.00	0.00	0.00
0.88	0.25	0.46	0.25	0.21	0.25	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00
0.44	0.25	1.38	0.74	0.21	0.25	0.40	0.31	1.67	0.00	2.43	2.08	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.84	0.00	0.35	0.00	0.49
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.88	0.98	0.00	0.25	1.26	0.25	0.40	0.15	0.00	0.38	0.35	0.35	0.00
0.44	0.25	0.00	0.00	0.00	0.00	0.40	0.15	1.26	0.76	1.04	2.08	2.44
0.44	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continued)

TABLE 2. (*continued*)

	Relative frequencies									
Fossil taxa	EM1	EM2	EM3	EM4	EM5	EM6	EM7	EM8	EM9	EM10
Intratriporopollenites sp.	0.00	0.00	0.00	0.00	0.39	0.40	0.00	0.34	0.00	0.00
Liliacidites sp. 1	0.00	0.27	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.43
Liliacidites sp. 2	0.23	0.27	0.00	0.00	0.00	0.40	0.35	0.00	0.00	0.00
Liliacidites sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. comodoroensis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.41	0.43
M. tenuireticulatus	0.23	0.55	0.44	0.22	0.39	0.40	0.70	0.00	0.00	0.00
M. vanwijhei	0.00	0.00	0.00	0.00	0.39	0.40	0.35	0.68	0.83	0.43
Margocoporites sp. 1	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.34	0.00	0.00
M. argentina	0.23	2.75	1.11	6.07	1.18	1.58	1.05	2.73	0.83	0.43
M. patersonii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M. viteauensis	0.23	0.27	1.11	0.67	0.39	0.40	0.35	0.34	0.41	0.43
Myrtaceidites sp.	0.23	0.00	0.22	0.45	0.00	0.40	0.35	0.34	2.07	0.00
M. verrucosus	0.23	0.27	0.22	0.00	0.79	0.40	0.70	1.02	0.00	0.00
N. acromegacanthus	0.69	4.40	2.44	2.02	0.79	0.40	3.48	1.37	3.73	3.85
N. americanus	0.46	0.27	0.44	0.22	0.79	0.40	0.35	2.05	0.83	3.42
N. dorotensis	0.23	0.00	0.22	0.22	0.39	0.79	0.35	0.00	0.00	0.43
N. flemingii	0.69	1.92	0.89	1.57	0.39	0.40	1.05	1.37	0.00	0.43
N. saraensis	0.92	7.69	10.64	6.07	8.66	5.53	6.97	5.12	5.35	9.83
N. tehuelchesii	0.00	0.00	0.67	0.22	0.00	0.00	0.70	0.00	0.00	0.43
N. endobalteus	0.00	0.00	0.00	1.12	2.36	2.37	2.09	0.34	0.41	0.00
Orapollis sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orapollis sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orapollis sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perforotricolpites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. vivianae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. pokornyi	0.00	0.00	0.00	0.22	0.39	0.00	0.00	0.00	0.00	0.00
P. puntensis	0.23	0.00	0.44	0.22	0.39	0.40	0.35	1.02	0.41	0.00
Polyadopollenites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polycolpopollenites sp.	0.00	0.00	0.22	0.22	0.39	0.40	0.35	0.00	0.00	0.43
Polycolporopollenites sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. obscurus	0.00	0.00	0.22	0.00	0.00	0.40	0.35	0.00	0.41	0.00
P. pseudomoides	0.23	0.00	0.22	0.00	0.39	0.40	0.35	0.34	0.00	0.85
Proteacidites sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.00	0.41	0.85
P. couperi	0.23	0.27	0.44	0.22	0.39	0.00	0.35	0.00	0.83	0.43
Psilatricolpites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. operculatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. protrudens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43
P. quenua	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Psilatricolporites sp.	0.46	0.00	0.89	0.22	0.39	1.58	0.70	0.68	0.00	0.43
Q. gamerroi	0.00	0.55	0.00	0.00	0.00	0.79	0.70	0.34	0.00	0.00
Q. stuessyi	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Q. tayuoides	0.00	0.27	0.22	0.22	0.00	0.00	0.00	0.00	0.00	0.00

EM11	EM12	EM13	EM14	EM15	EM16	EM17	EM18	LM19	LM20	LM21	LM22	LM23
0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	2.70	0.42	1.25	1.20	1.68	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.46	0.25	0.42	0.25	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.74	0.00	0.25	0.21	0.25	0.40	0.46	0.00	0.00	0.00	0.00	0.49
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.67	0.38	1.04	1.33	0.49
0.44	0.74	0.46	1.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.15	0.00	0.00	0.35	0.00	0.00
0.44	1.23	0.00	0.25	1.05	0.25	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	0.00	0.21	0.25	0.40	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
10.13	3.69	13.76	2.70	4.82	1.00	2.41	4.44	0.00	0.00	0.00	1.04	0.00
1.32	0.25	2.29	0.49	0.84	0.75	1.20	0.46	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.25	9.09	17.43	22.55	9.22	16.50	7.23	14.55	5.01	5.33	8.33	6.57	3.41
0.44	0.00	0.46	0.74	0.00	0.00	0.00	0.61	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.23	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.46	0.84	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.15	0.42	0.00	0.00	0.00	0.00
0.44	0.98	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00
0.00	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.76	0.38	0.00	0.00
0.44	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.25	0.21	0.25	0.40	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.38	1.04	0.49	0.98
0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.84	0.00	0.00	0.35	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.00	0.00	0.63	0.00	0.40	0.15	0.42	0.38	0.35	0.35	1.95
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.38	0.35	0.35	0.49
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE 2. (*continued*)

	Relative frequencies									
Fossil taxa	**EM1**	**EM2**	**EM3**	**EM4**	**EM5**	**EM6**	**EM7**	**EM8**	**EM9**	**EM10**
Q. striatulosa	0.23	0.27	0.22	0.22	1.18	0.40	0.35	0.34	1.24	0.00
R. cienaguensis	0.00	0.27	0.00	0.67	0.39	0.00	0.35	1.37	0.41	0.43
R. romeroi	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.34	0.00	0.43
R. baculatus	0.23	0.27	0.67	2.02	0.39	1.98	0.35	1.37	1.24	0.85
R. minusculus	0.23	0.27	0.67	0.22	0.39	1.98	0.35	0.34	2.49	0.43
Rhoipites sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.43
Rhoipites sp. 2	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhoipites sp. 3	0.00	0.00	0.00	0.00	1.18	0.00	0.00	0.00	0.00	0.00
Rhoipites sp. 4	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhoipites sp. 5	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00
R. oblatus	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00
S. patagonica	0.00	0.27	1.77	0.22	0.39	1.19	0.35	2.39	1.66	2.14
S. barungensis	0.69	0.82	0.44	0.67	0.39	0.40	1.39	2.05	0.41	0.43
S. sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sparsipollis sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S. garnerroi	0.92	1.37	0.22	2.47	5.91	4.35	4.18	5.46	2.49	0.43
Striatricolporites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thymelaepollis sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. reticulatus	0.46	0.27	0.22	0.45	0.39	0.40	0.35	0.34	0.41	0.43
T. tnoblatus	1.14	0.27	0.44	0.22	0.00	0.00	0.00	0.34	1.66	1.28
Tricolpites sp. 1	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00	0.00	0.00
Tricolpites sp. 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00
Tricolpites sp. 3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tricolpites sp. 4	0.00	0.27	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. minor	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triporopollenites sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. antipodica	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. pleistocenicus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. simplis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Ephedra, composites, and a species of amaranth. Other monocots (i.e., Cyperaceae, Thyphaceae) and dicots (i.e., Malvaceae, Onagraceae, Proteaceae) occupy an intermediate position (Fig. 4)

PLANT RICHNESS

Measures of diversity (rarefaction, Shannon-Wiener and Simpson indices, standing diversity) show a sustained decrease from the Early to the Late Miocene (Figs. 5–7, Table 3). The rarefaction analyses indicate that the spore-pollen assemblages of selected samples representing the Early Miocene (Group A) are significantly richer (Tukey test, Fig. 7) than those for the Late Miocene (Group B) (Figs. 5, 6). Nearly the same rarefaction curves result if all the curves of groups A and B are plotted (not shown), and thus the high diversity observed in the Early Miocene does not depend on a single sample or on the aggregation of numerous samples. The highest values of rarefied species

EM11	EM12	EM13	EM14	EM15	EM16	EM17	EM18	LM19	LM20	LM21	LM22	LM23
0.44	0.25	0.46	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.32	1.72	0.46	0.98	0.42	0.50	1.20	0.46	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.32	0.25	0.46	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.76	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1.32	0.25	0.00	0.25	0.00	0.00	0.40	0.00	1.26	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.49
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.04	0.35	0.49
0.88	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00
3.96	0.49	0.46	1.47	0.21	0.75	0.00	0.31	0.00	0.00	0.00	0.00	0.00
1.76	3.19	1.38	4.66	2.10	2.50	1.20	2.45	10.04	17.11	3.47	10.03	0.98
0.00	0.00	0.00	3.68	3.56	5.75	2.81	5.21	0.00	0.00	0.00	0.00	0.00
0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	1.23	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.84	0.25	1.20	0.77	0.42	5.32	1.39	3.46	2.44
0.44	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.25	0.46	0.25	0.21	0.50	0.40	0.46	0.00	0.00	0.00	0.00	0.00
0.88	4.67	2.29	2.70	2.94	3.00	2.41	4.13	1.26	3.42	8.68	4.15	6.83
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.44	0.00	0.00	0.25	0.00	0.00	0.40	0.31	0.00	0.00	0.00	0.35	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.25	0.42	0.25	1.20	0.92	2.51	0.76	0.69	1.38	2.44
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.38	1.04	1.04	0.98
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.76	1.39	0.35	0.49

richness occur in the Early Miocene samples (Group A), while the lowest values occur in the Late Miocene samples (Group B, Fig. 5). The rarefied richness at 200 specimens is 63 and 64 species in Samples EM7 and EM10, respectively (Group A1, Early Miocene), and 22 species in Sample LM20 (Group B, Late Miocene) (Fig. 6). Comparable values are obtained using other measures of diversity (Shannon-Wiener and Simpson indices and standing diversity) as depicted in Table 3 and Figure 6. The most diverse samples (Group A) yielded abundant palynomorphs assigned to forest taxa (e.g., Nothofagaceae, Podocarpaceae, Fig. 6D). The samples containing the highest diversity values within Group A1 (e.g., EM7) yielded a number of palynomorphs assigned to warm-loving taxa (e.g., Malvaceae [Bombacoideae], Sapindaceae, Arecaceae, and Malpighiaceae: Barreda, 1996, 1997a–1997d). In contrast, the least diverse samples (Group B) yielded abundant

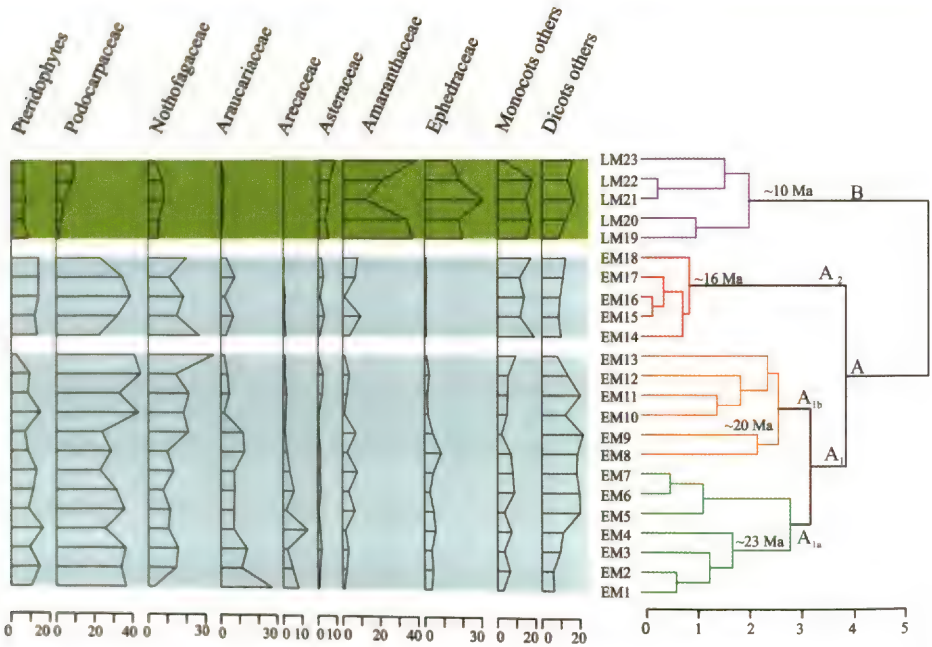

FIGURE 3. Spore and pollen diagram shown as percent abundance in a sample from Miocene deposits of eastern Patagonia (Chenque and Puerto Madryn formations). The "coniss" cluster dendrogram at right displays distinct, stratigraphically ordered sample groups. Blank zones in the spore and pollen diagram represent temporal intervals without palynological records. Note the large Late Miocene decrease in conifer, southern beech, and fern abundances and a parallel increase in amaranth, *Ephedra*, and Asteraceae abundances. Early Miocene groups: A1a (samples EM1–EM7, green lines), A1b (samples EM8–EM13, orange lines), A2 (samples EM14–EM18, red lines). Late Miocene group: B (samples LM19–LM23, violet lines).

arid- to semiarid-adapted taxa (e.g., Ephedraceae and Amaranthaceae, Fig. 6D).

Quantitative comparisons of rarified species richness of the groups defined by the cluster analysis show no significant differences between the Early Miocene groups A1 and A2, while that of the Late Miocene, Group B, is significantly different from those of the Early Miocene (ANOVA, F value = 16, $P = 0.000119$; for post hoc Tukey tests, see Fig. 7).

The overall decline in diversity is also recorded when the major taxonomic groups (i.e., ferns, gymnosperms, and angiosperms) are analyzed (Fig. 8). Ferns and gymnosperms are extensively more abundant and diverse in Early Miocene samples (Group A) than in Late Miocene samples (Group B, Fig. 8, Tables 2, 3). Angiosperms, although following a similar pattern of diversity, are far more abundant in samples of the Late Miocene (Group B) than in samples of the Early Miocene (Group A).

The species accumulation curves show a similar rate of increase in the overall number of species among the Early Miocene groups (groups A1a, A1b, A2) defined by the cluster analysis, while that of the Late Miocene (Group B) shows a slower increase (Fig. 9).

DISCUSSION

Our study allowed us to quantitatively estimate, for the first time for southern South America, species diversity (e.g., relative to sample size, to pollen abundance, and to facies shifts) across

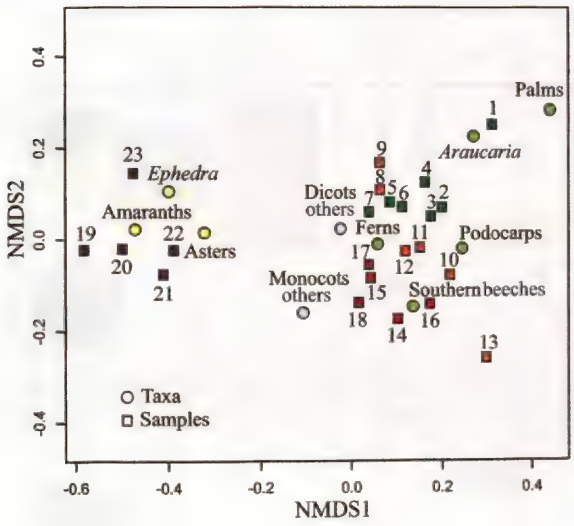

FIGURE 4. Results of non-metric multidimensional scaling (NMDS) ordination of spore-pollen data from Miocene deposits of eastern Patagonia (Chenque and Puerto Madryn formations). Sample numbers, square colors, and sample groups are explained in Figure 3. Stress = 0.073. Light green circles = humid-adapted taxa; yellow circles = arid-adapted taxa; gray circles = other taxa.

the Miocene based on fossil pollen assemblages. The resulted estimations led us to infer that significant changes in the eastern Patagonian flora occurred throughout the Miocene, with the development of two clearly different plant ecosystems: a highly diverse forested biome during the Early Miocene, and a significantly less diverse shrubby-herbaceous biome during the Late Miocene. The major peak in diversity obtained from the spore-pollen record occurred in the Early Miocene (Group A1, Fig. 6). Interestingly, it was during this time interval when many of the warm-loving taxa were recorded (e.g., *Cupania*, Malvaceae [Bombacoideae], *Ilex*) or were most frequent (e.g., palms), thus suggesting conditions were equable and frost-free at the time. The most striking feature of this Early Miocene peak of diversity is that it is not only the Miocene's highest value obtained from the spore-pollen record here analyzed, but it involves all major taxonomic groups (e.g., ferns, gymnosperms, and angiosperms). This simultaneous rise in diversity may have resulted from the combination of several events, including the immigration of north-

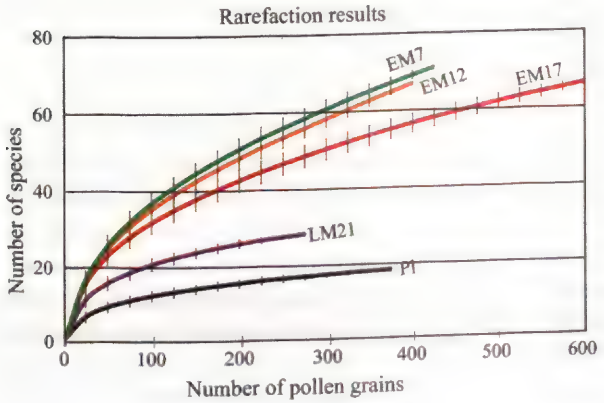

FIGURE 5. Rarefaction results from spore-pollen counts of selected samples representing groups A1a, A1b, A2 (Early Miocene) and Group B (Late Miocene). Groups and curve colors are explained in Figure 3. Pleistocene spore-pollen diversity values (black line labeled P1) are lower than any other here compared, revealing a progressive but sustained decline in diversity of the eastern Patagonian flora through the Neogene. Note that rarefaction curves provide information on both richness and evenness, hence the decline in richness is genuine and not just an effect of changing relative abundance distributions.

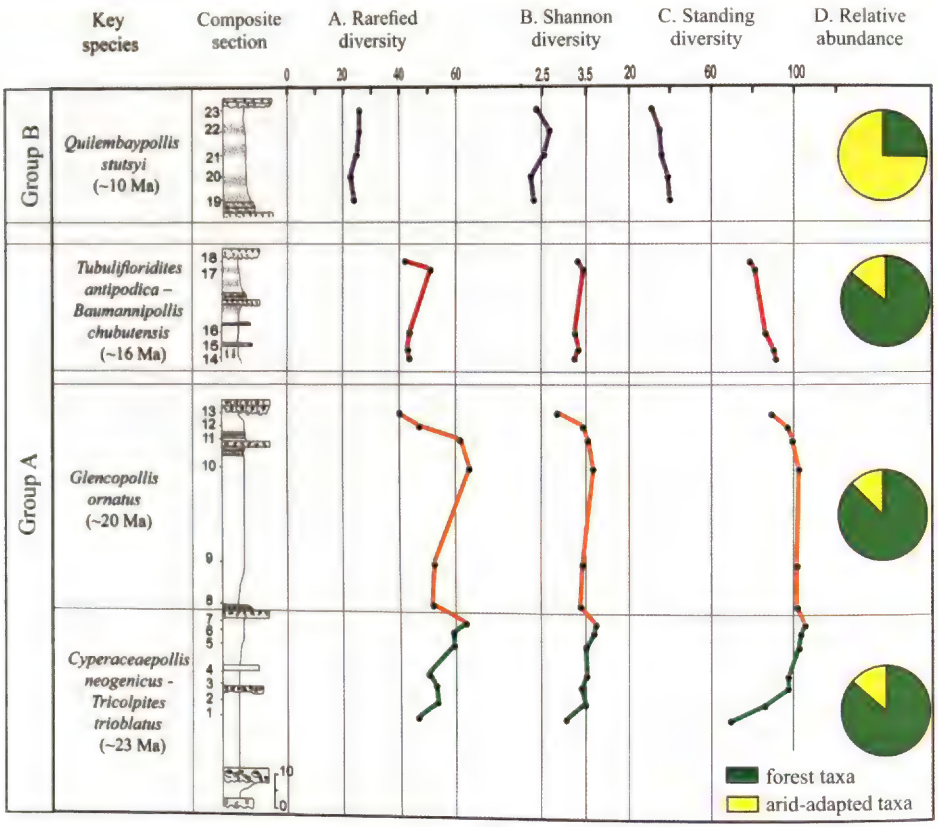

FIGURE 6. Quantitative distribution of spore-pollen species from Miocene deposits of eastern Patagonia (Chenque and Puerto Madryn formations) according to selected diversity indices. —A. Rarefied species richness of spore-pollen assemblages at 200 specimens. —B. Shannon-Wiener index curve. —C. Standing diversity curve. —D. Pie charts showing the relative abundance of forest versus shrub-herbaceous groups. Taxa recorded in only one sample were excluded. Curve colors are explained in Figure 3. Values in part A (0 to 60) are number of species, values in part B (2.5 to 3.5) are different values of diversity measured with the Shannon-Wiener index, values in part C (20 to 100) are "number of species" measured with standing diversity, a measurement that assumes that a taxon is present in a sample if it is found both above and below it.

ern South American lineages (e.g., Malpighiaceae), the conservative persistence of Gondwanan plant families (e.g., Nothofagaceae, Myrtaceae, Casuarinaceae), and the in situ speciation of relatively modern groups (e.g., Vivianiaceae, Asteraceae, Fabaceae). Other biological forces such as low extinction rates and, particularly, climatic (e.g., warming phases) forces may have also contributed to the high diversity values demonstrated. It is worth mentioning that rarified values of diversity seem to be comparable to those recorded elsewhere in South and North America, even during the warmest periods of the Cenozoic (e.g., Jaramillo, 2002; Wilf et al., 2003; Harrington, 2008; Jardine et al., 2012; Mejía et al., 2012), although this hypothesis needs to be tested by an increased sampling effort (Barreda & Palazzesi, in prep.). During the Early Middle Miocene (Group A2) some warm-loving taxa persisted (e.g., *Cupania*, Malvaceae [Bombacoideae]), although diversity values slightly decreased. This suggests that the Miocene warm phase may not have been the

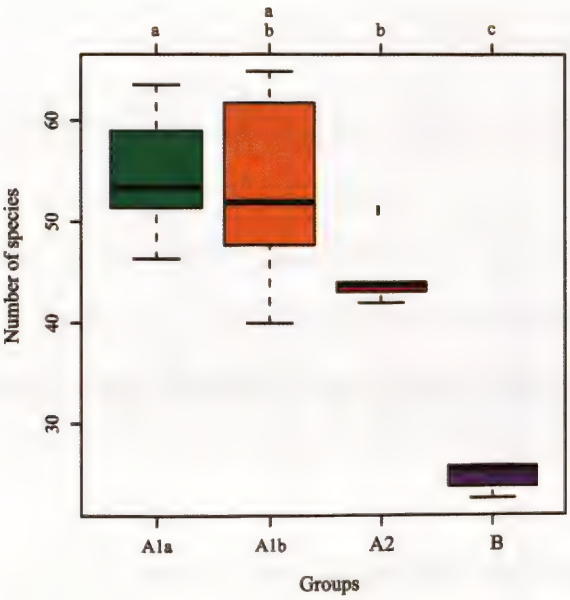

FIGURE 7. Rarefied richness expressed as box plots in relation to groups of samples for the overall number of species for Miocene assemblages. Results from the post hoc Tukey test are shown, with columns labeled a, ab, b, and c to denote significant differences among group means. The group labeled "ab" was not significantly different from either the group labeled "a" or the one labeled "b." Horizontal midlines represent the median.

sole trigger of diversity, and indicates a more complex origin for the Early Miocene peak.

A significant drop in diversity occurred from the Early to the Late Miocene, as indicated by a long decline in diversity of important, previously dominant tree taxa such as southern beeches and podocarps, but also by a rise of shrubs tolerant of arid conditions, such as Ephedraceae and Amaranthaceae. Overall, from the Early to the Late Miocene at least 24 families and a minimum of 43 genera were lost from the eastern Patagonian flora. They included climatically sensitive key groups, both temperature-sensitive Neotropical taxa (e.g., *Ilex*, *Cupania*, *Alchornea* Sw., *Symplocos* Jacq., and several palms) and humidity-sensitive Gondwanan taxa (e.g., *Dacrycarpus*, *Dacrydium*, *Lagarostrobus*, *Microcachrys*). Today, these Neotropical and Gondwanan taxa occupy much warmer (mean annual temperature [MAT] ~25°C) and moister (~2000 mm average annual precipitation) regions, respectively. The extinctions appear to have been highly selective, including a range of life forms (higher among trees, vines, and ferns), and were simultaneous sometime in the mid-Miocene. Amaranthaceae, *Ephedra*, *Chuquiraga* Juss., *Schinus* L., and *Prosopis* L. are all environmentally stress-adapted taxa that survived the onset of aridization of the Late Miocene. Moreover, Ephedraceae and Amaranthaceae abruptly rose in abundance in the Late Miocene, with a 10-fold increase of the former and a 36-fold increase of the later, representing one of the major turnovers in Patagonian communities toward a more open and modern vegetation. After this major interruption of the non-Andean vegetation, angiosperms became far more abundant than pteridophytes and gymnosperms for the first time. In addition to the amaranth family, the composites (e.g., Nassauviinae and Barnadesioideae) contributed to the overall increase in angiosperm abundance. Today, members of these last two lineages, i.e., *Nassauvia* Comm. ex Juss. and *Chuquiraga*, grow along the coast in eastern Patagonia and survive under strong winds and marine spray.

The potential relationship between environmental variables, such as temperature and humidity, and shifts in diversity (either due to immigration

TABLE 3. Diversity data. The lack of significant variations in the evenness values through the Miocene may be more related to differences in pollen productivity among taxa than the absence of true dominant parent plants in a community (e.g., Bush & Rivera, 2001).

	Diversity values							
S	Gc	R	Sh	Sm	Ev	St	Or	Ex
LM23	205	25.78	2.37	0.82	0.50	31	0	13
LM22	289	25.74	2.68	0.9	0.56	35	1	4
LM21	288	25.43	2.54	0.87	0.54	36	0	2
LM20	263	22.56	2.24	0.82	0.57	39	2	3
LM19	239	23.74	2.30	0.82	0.57	40	4	3
EM18	653	41.93	3.31	0.94	0.60	78	4	42
EM17	249	51.05	3.43	0.95	0.59	81	1	7
EM16	400	43.93	3.24	0.93	0.56	86	1	6
EM15	477	43.02	3.32	0.95	0.58	90	3	5
EM14	408	43.71	3.23	0.92	0.59	91	8	4
EM13	218	39.92	2.81	0.9	0.59	89	1	6
EM12	407	47.66	3.43	0.95	0.56	97	1	9
EM11	227	61.70	3.55	0.95	0.52	99	1	3
EM10	234	64.81	3.65	0.96	0.55	102	2	4
EM9	241	52.32	3.40	0.94	0.56	101	1	1
EM8	293	51.46	3.35	0.93	0.55	101	3	1
EM7	286	63.49	3.72	0.96	0.59	105	5	7
EM6	253	58.83	3.65	0.96	0.54	103	2	3
EM5	254	59.05	3.48	0.95	0.50	102	8	1
EM4	445	50.05	3.50	0.95	0.48	97	5	3
EM3	451	52.66	3.38	0.94	0.53	97	13	5
EM2	364	53.35	3.47	0.95	0.55	85	17	1
EM1	437	46.30	3.03	0.89	0.50	69	0	1

Abbreviations: S = sample number; Gc = grains count; R = rarefaction 200 grains cutoff; Sh = Shannon-Wiener index values; Sm = Simpson index values; Ev = evenness (Pielou's J index); St = standing diversity values; Or = origination values; Ex = extinction values.

and/or low extinction rates) may be misrepresented due to inaccuracies in the chronology of the composite section. Yet, positive peaks in the rarefied and the standing diversity pollen curves (Fig. 6) broadly coincide with those of the oxygen-isotope curve (e.g., Miocene Climatic Optimum, Zachos et al., 2001).

The strong decline in Late Miocene diversity most likely followed the Middle Miocene expansion of the Antarctic ice sheet, a decrease in atmospheric pCO_2, and the subsequent drop in temperature (Badger et al., 2013), and also paralleled the marked increased aridity caused by the Andean uplift. The uplift may have led to an intensification of the orographic rain shadow after about 14 million years ago (Ma) (Blisniuk et al., 2005; Palazzesi et al., 2014). Overall, global cooling trends and increasing aridity appeared to have acted as major environmental filters in the composition and structure of the eastern Patagonian flora, promoting regional extinctions and decreasing plant diversity. Further detailed sampling in new areas will be crucial for obtaining a more refined relationship between floristic richness and

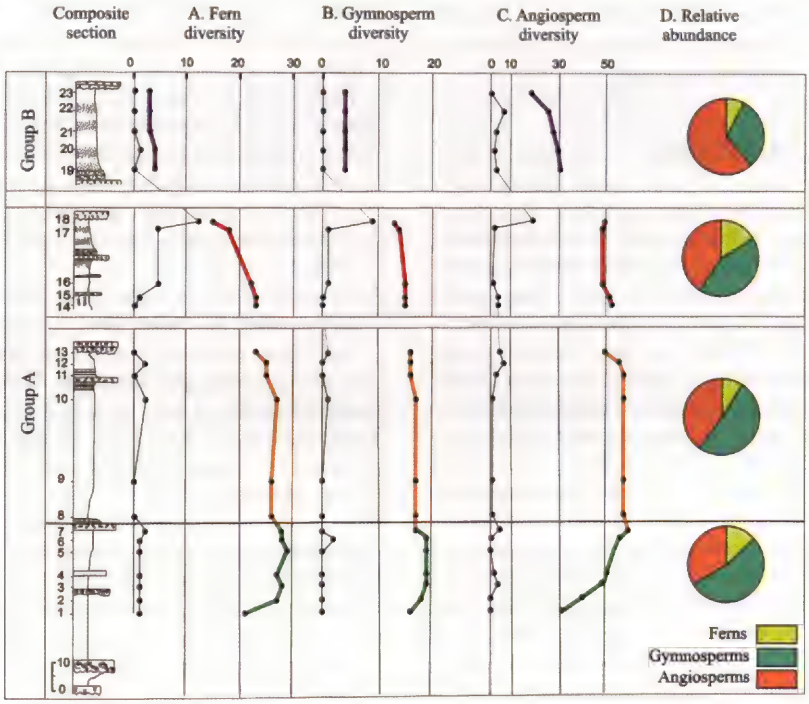

FIGURE 8. Quantitative distribution of major plant groups from Miocene deposits of eastern Patagonia (Chenque and Puerto Madryn formations). —A. Fern diversity. —B. Gymnosperm diversity. —C. Angiosperm diversity. Curves are based on standing diversity richness; upper margin values refer to the number of species. Curve colors are explained in Figure 3. The extinction curves (black lines) show a marked decline in the number of taxa from the Early to the Late Miocene. —D. Pie charts showing the relative abundance of major plant groups (ferns, gymnosperms, angiosperms).

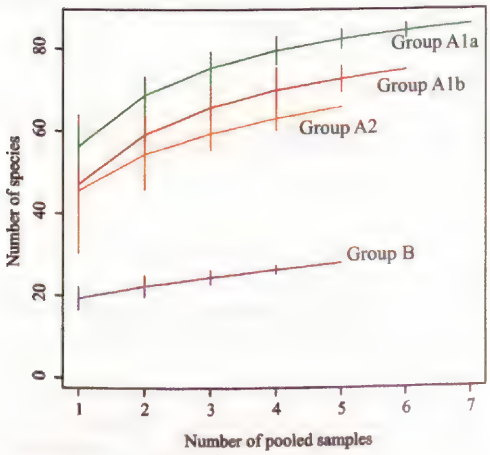

FIGURE 9. Species accumulation curves for the overall number of species for Miocene groups. Curve colors are explained in Figure 3.

paleoclimate. This quantitative approach, however, represents the first diversity estimation for the Miocene of southern South America and provides a new basis with which to better understand the complex origins and evolution of the extant Patagonian flora.

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CHAPTER 2

A NEW LEAF IN THE GENUS *INGA* (FABACEAE) IN EOCENE SEDIMENTS OF THE LA CARROZA FORMATION, LA POPA, NUEVO LEÓN, MEXICO, WITH COMMENTS ON ITS BIOGEOGRAPHIC IMPLICATIONS

Laura Calvillo-Canadell, Sergio Rafael Silvestre Cevallos-Ferriz, and Mario Sousa-Sánchez*

ABSTRACT

The fossil flora of the Eocene La Carroza Formation, Nuevo León, Mexico, has yielded a number of plants with diverse biogeographic origins that are indications of two distinct tropical biomes, a warm and dry one and a warm and humid one. A new leaf is herein described as *Inga eocenica* Calvillo-Canadell, Cevallos-Ferriz & Sousa-Sánchez, based on its compound structure with winged rachis and interpetiolar nectaries; opposite, elliptic-ovate to lanceolate leaflets with rounded-convex asymmetric bases; straight to acuminate apex; pulvinate petiolule; pinnate primary venation; eucamptodromous secondary venation; and irregular reticulate third- and fourth-order venations. These characters are not definitive but may suggest that the species was growing under drier conditions within a warm temperate to subtropical environment. Its presence is important to further discussions on the time and manner in which the Mexican flora became integrated, and suggests that the dry elements were selected from humid communities. A fruit assigned to *I. popensis* Calvillo-Canadell & Cevallos-Ferriz, and previously reported from the same locality, may represent the same plant. This evidence for the presence of a Neotropical plant earlier than expected according to some biogeographical hypotheses suggests that the exchange of floras between the Americas during the Cenozoic may have started as early as the Eocene, and that the integration of extant floras like the Neotropical flora was due to a complex process, in which the sources of its components remain unclear.

Key words: Eocene, Fabaceae, *Inga*, Ingeae, Mexico, Mimosoideae, Oligocene.

Through time, Mexico has had a geographic position that allowed convergence of biotas from different parts of the world, which resulted in an interesting mix of plant communities. This was evident during the Cenozoic, and it is well known especially for more recent times, because the extant biota has been well documented and discussed as a result of interest in the convergence of Nearctic and Neotropical elements. However, the mechanisms and processes that facilitated the establishment of taxa in Mexico from different geographic sources are still an active topic of study.

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Interest in the biota of Mexico can be traced to at least the 1600s, when Hernández (1651) and Sessé y Lacasta and Mociño (1891–1897, 1894) described many species, especially those with economic importance. Rzedowski (1978) summarized this story, highlighting the travels of De Lafora (1939) between 1766 and 1768. Later, the main characteristics of the flora of Central Mexico were described by Hartweg (1842) and, almost simultaneously, by Liebmann (1844), who reported on the flora from the Port of Veracruz to the peak of Orizaba. Berlandier and Chovel (1850) described the flora from Mexico City to Texas, while Seemann (1852–1857) wrote of the flora of the west coast of Mexico. The first descriptions of phytogeographical zonation of Mexico were proposed by Martens and Galeotti (1842) and Richard and Galeotti (1844). From the mid-19th century onward, understanding of the diverse biota of the region grew rapidly (e.g., Herrera, 1869; Grisebach, 1877–1878; Hemsley, 1879–1888; Ramírez, 1899; Harshberger, 1911; Ochoterena, 1923, 1937; Shelford, 1926). Throughout the 20th century botanical work continued, focusing on small areas or states as well as on vegetation types (Rzedowski, 1978). Beginning in the 1950s and thereafter, the information on vegetation was summarized in the form of biogeographic maps and in comparative tables of different vegetation classifications (e.g., Smith & Johnston, 1945; Leopold, 1950; Miranda & Hernández-X., 1963; Gómez-Pompa, 1965; Flores et al., 1971; González-Medrano, 2003). These works include different kinds of geologic information, sometimes only incidentally; none discuss the geology linked to the vegetation. In a few cases the fossil record was discussed chronologically to improve the understanding of the flora from a historical point of view (e.g., Berry, 1923; Brouard & Marty, 1923; Deevey, 1943; Rzedowski, 1962; Miranda, 1963; Langenheim, 1966; Langenheim et al., 1967; Rueda-Gaxiola, 1967; Graham, 1973a, 1973b, 1992b; Ohngemach, 1973).

In the second half of the 20th century a great effort was made to generate a more comprehensive and strongly supported hypothesis about the origins of vegetation in Latin America, an effort led by Alan Graham. One of the merits of this initiative was to consolidate information from both paleobotanical and neobotanical research (e.g., Graham, 1973a, 1973b, 1976, 1992a, 1992b, 1999, 2010; Graham & Dilcher, 1995; Graham & Palacios-Chávez, 1996; Burnham & Graham, 1999). Graham recognizes as one mechanism for the integration of the Mexican flora the Great American Biotic Interchange, but he also recognizes that a more complex history may be involved. While Graham's ideas were proposed at a time when information on the fossil floras of Mexico was scarce and mainly limited to few palynological data sets (e.g., Miranda, 1963; Espinosa de G. Rul & Rzedowski, 1968; Ohngemach, 1973, 1977; Rzedowski & Palacios-Ch., 1977; González Quintero & Fuentes Mata, 1980; Martínez-Hernández et al., 1982a, 1982b; Martínez-Hernández, 1992; Martínez-Hernández & Ramírez-Arriaga, 1999; Ramírez-Arriaga et al., 2005), most have been borne out of subsequent studies. In the last decades information has grown and data on macrofossils have been incorporated (e.g., Magallón-Puebla & Cevallos-Ferriz, 1994a, 1994b; Hernández-Castillo & Cevallos-Ferriz, 1999; Ramírez et al., 2000; Ramírez & Cevallos-Ferriz, 2002; Calvillo-Canadell & Cevallos-Ferriz, 2002, 2005, 2007; Estrada-Ruiz & Cevallos-Ferriz, 2007; Estrada-Ruiz et al., 2007). The expanded data do support a complex biogeographic history for the region, and that history is just now being untangled. Biological processes inducing diversification and radiation, as well as expansion and reduction of distribution areas, are clearly linked to the complex geological history of the country (Cevallos-Ferriz et al., 2012). We exemplify this situation by describing here a new species of *Inga* Mill. based on leaf material, and we suggest that this compound leaf

type may represent the vegetative part of a fossil plant that produced fruits earlier identified as *I. popensis* Calvillo-Canadell & Cevallos-Ferriz. The proposed reassembled plant is used to discuss the biogeographic implications of this record; a more detailed biogeographical study of this problem will be presented elsewhere.

MATERIAL AND METHODS

The fossils were collected in the Eocene La Popa locality in Nuevo León, where the La Carroza Formation outcrops (Fig. 1A; Vega-Vera et al., 1989). A total of five fossils were analyzed. They contain impressions of a leaf and isolated leaflets with different degrees of conservation.

The Nuevo León outcrop is composed of more than 600 m of red layers comprising shales and medium-grained sandstones containing fossils. The presence of terrigenous rocks in this formation and in the Difunta Group, to which the La Carroza Formation belongs, complicates its dating. Some nonmarine rocks of this sequence are very well dated by radiometrics or mammal biostratigraphy; however, these materials have not been found in the La Carroza Formation, and the age of the sequence is suggested as Middle Eocene based on geological observations and stratigraphic ranges of invertebrate fossils collected in the underlying formations (Andrie et al., 2010). The locality is found near San José de la Popa, Nuevo León, between lat 26°00′N and 27°00′N and between long 100°30′W and 101°00′W.

All fossils used in this study are deposited in the Paleontological Collection of the Institute of Geology, Universidad Nacional Autónoma de México (UNAM). When necessary, the material was mechanically cleaned with an air scriber in order to completely expose the fossils. The characters of the impression fossils were observed directly and with the aid of an Olympus SHZ stereoscopic microscope, sometimes employing a camera lucida to draw the fossils. Photography was basic to the development of the project. Occasionally, submerging the fossils in water, alcohol, or acetone enhanced the features, allowing more and better information to be obtained. Photographs were taken with a Sony (Tokyo, Japan) digital camera model D11. The taxonomic affinities of the fossil organs were established by comparison to organs of extant plants in the MEXU collections.

The terminology employed for leaf architecture follows Hickey (1973, 1979), Hickey and Wolfe (1975), and the manual of the Leaf Architecture Working Group (1999).

SYSTEMATICS

Family: Fabaceae

Subfamily: Mimosoideae

Tribe: Ingeae

Genus: *Inga* Mill.

Section: *Pseudinga* Benth.

Species: ***Inga eocenica*** Calvillo-Canadell, Cevallos-Ferriz & Sousa-Sánchez, sp. nov.

Holotype: designated here: Paleontological Collection of the Institute of Geology, UNAM, catalog number IGM-5463 (Fig. 2A).

Paratype: designated here: Paleontological Collection of the Institute of Geology, UNAM, catalog number IGM-6538.

Type locality: Near the town of San José de la Popa, Nuevo León, Mexico, between lat 26°00′N and 27°00′N and between long 100°30′W and 101°00′W.

Stratigraphy and age: The La Carroza Formation of the Difunta Group, Eocene.

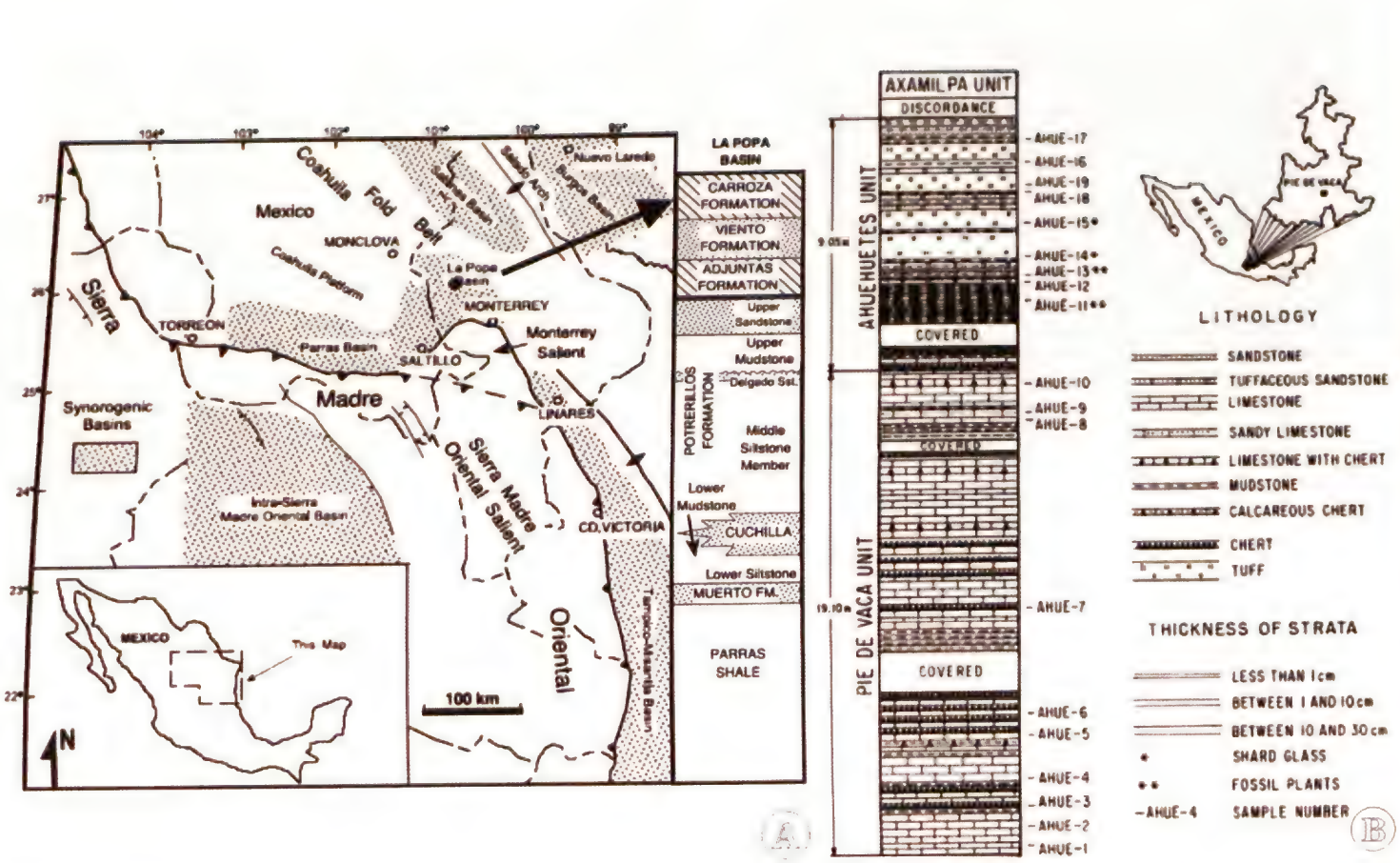

FIGURE 1. —A. Location of the La Popa locality, La Carroza Formation, showing the paleobotanical site. Map modified from Soegaard et al. (2003). —B. Stratigraphic column of the Los Ahuehuetes locality where Oligocene *Inga* leaf and fruit have been collected. Modified from Calvillo-Canadell and Cevallos Ferriz (2002).

Etymology: The specific epithet refers to the geologic age of the layer in which the material was found.

Number of examined specimens: One nearly complete leaf and five isolated leaflets.

Diagnosis: Compound leaf with winged rachis and interpetiolar nectaries; opposite, elliptic-ovate to lanceolate leaflets with rounded-convex asymmetric base, straight to acuminate apex, pulvinate petiolule, pinnate primary venation, eucamptodromous secondary venation and irregularly reticulate third and fourth order venations.

Description: The material comprises one incomplete (Fig. 2A, B) compound fossil leaf and several dispersed leaflets. The leaf has 5 opposite lateral leaflets (Fig. 2A, B) with pulvinate petiolules (Fig. 2E) and a winged rachis ca. 7.0 cm long (Fig. 2B, E). The wings on the rachis are oblanceolate-obovate and 0.5 cm wide. Cup-shaped interpetiolar nectaries are present with a narrow aperture (Fig. 2C, D). The proximal left leaflet and distal right leaflet are complete, 4.7 × 1.7 cm and 6.7 × 1.5 cm, respectively. The other leaflets are incomplete and vary in size, but there is an increase in size distally. The lamina is symmetrical, although the base is slightly asymmetrical, with untoothed margins (Fig. 2A–F). The lamina is elliptic or ovate to lanceolate and the apex is acuminate to acute with an angle of 77°. The base is rounded-convex, forming an obtuse angle of 133° (Fig. 2A, B, F). The primary venation is pinnate; the major secondaries are eucamptodromous and their spacing decreases proximally (Fig. 2E). Ten to 12 pairs of secondary veins form an acute angle with respect to the midvein. The major secondaries are excurrent. The leaflets have well-preserved intersecondary veins with a proximal course parallel to major secondaries; their length is less than 50% of the subjacent secondary veins and there is more than one per intercostal area. The intercostal tertiary and quaternary vein fabric is irregular-reticular (Fig. 2F). Additional levels of venation are not observed due to the nature of the material.

Comparison with extant taxa: The compound nature of the leaf, as well as the presence of pulvinate leaflets, suggests some relationship of the fossil with the Fabaceae. Furthermore, the presence of a winged rachis, interpetiolar nectaries, and the venation pattern strongly suggest that the fossil represents a member of *Inga* (Fig. 3). Although the fossil is generally similar to leaves of *Bursera* Jacq. ex L. (Burseraceae), the nectaries and the venation pattern of the fossil leaflets clearly separate them.

While the characteristics of the fossil support the recognition of *Inga*, its placement in an infrageneric taxon is more complicated, since all sections have both winged and unwinged species. The number of paired leaflets suggests that the plant that produced the leaf is a member of section *Pseudinga*, where the number of pairs varies from three to six (Pennington, 1997). Within this section, resemblance of the new fossil material is particularly close to *I. micheliana* Harms and *I. hintonii* Sandwith (Fig. 3). The presence of many diagnostic features allows *I. eocenica* to be closely compared to the other species: symmetrical, elliptical-ovate to lanceolate lamina with a slightly asymmetrical convex-round base; acute to acuminate apex; venation that includes the pinnate first order venation; eucamptodromous secondary order venation with intersecondary veins well developed; and third- and fourth-order irregular-reticular venation. These characters, along with the presence of the winged rachis, pulvinate petiole, and interpetiolar nectary support placement of the new fossils in *Inga* sect. *Pseudinga* as a new species. Age differences and limited information about the rest of the plant prevent assignment to an extant species.

Recognition of leaflets with *Inga* affinity in the La Carroza Formation is important because it is a new taxon for the flora of this locality, and be-

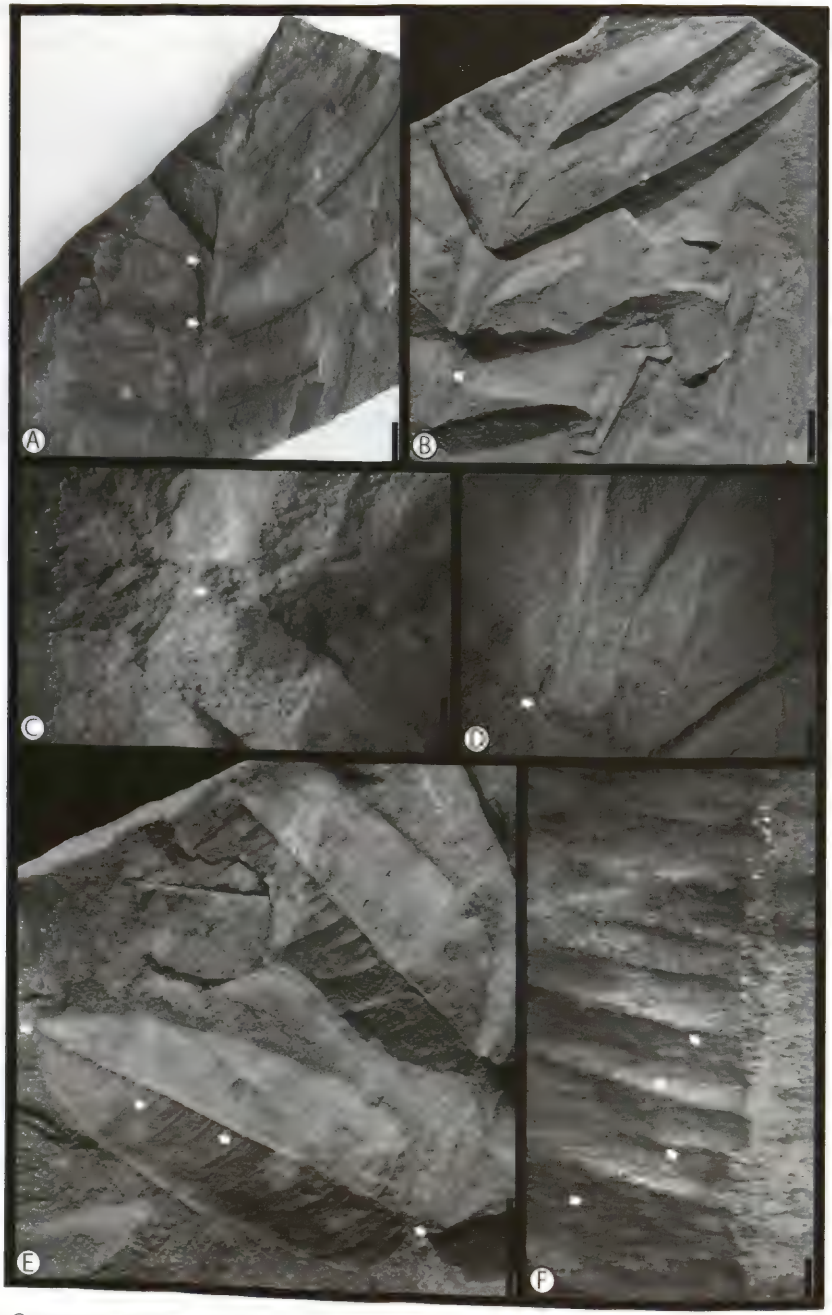

FIGURE 2. Compound leaf of *Inga eocenica*. —A. Nectary (lower arrow) and winged rachis (upper arrow). Scale = 1.0 cm. —B. Venation in winged rachis (arrow). Scale = 1.0 cm. —C. Nectary (arrow). Scale = 1.0 cm. —D. Pulvinate petiolule (arrow). Scale = 1.0 cm. —E. Convex rounded base (lower arrow), intersecondary venation (lower middle arrow), eucamptodromous secondary venation (upper middle arrow), acuminate to straight apex (upper arrow). Scale = 1.0 cm. —F. Reticular third order venation (lower arrow), major secondaries (two uppermost arrows), intersecondary vein (middle arrow). Scale = 1.0 mm.

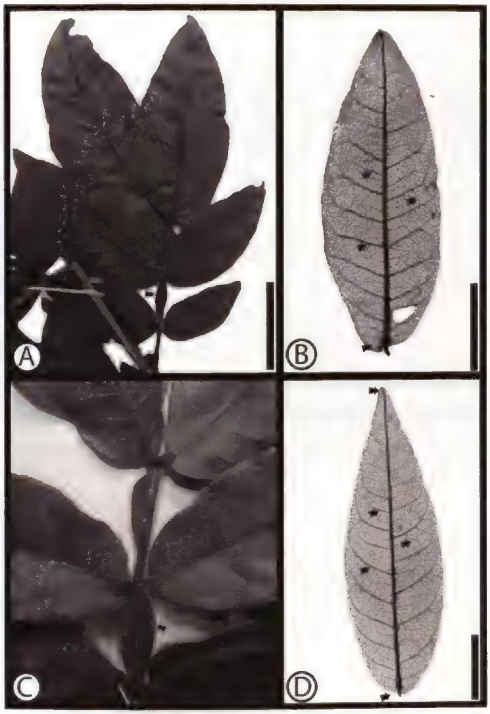

FIGURE 3. Extant leaves and leaflets of *Inga*. —A. Compound leaf of *I. micheliana* with winged rachis (arrow). —B. Cleared leaf of *I. micheliana* with rounded convex base (lowest arrow), eucamptodromous major secondaries (lower left middle arrow), irregular reticular third order venation (upper right middle arrow), and intersecondary vein (uppermost arrow). —C. Compound leaf of *I. micheliana* with winged rachis (lower arrow), interpetiolar nectary (middle arrow), and pulvinate petiolule (upper arrow). —D. Cleared leaf of *I. hintonii* with convex rounded base (lowest arrow), eucamptodromous major secondaries (lower left middle arrow), irregular reticular tertiary venations (right middle arrow), intersecondary veins (upper left middle arrow), and acuminate to acute apex (uppermost arrow). All scale bars = 1.0 cm.

cause a fruit assigned to the same genus was described previously (Calvillo-Canadell & Cevallos-Ferriz, 2005). The sectional affinities of the two organs differ. The leaves of *I. eocenica* relate by number of paired leaflets to section *Pseudinga*, and no leaves similar to *I. eocenica* are known from section *Inga*. Although inclusion of *I. eocenica* in section *Pseudinga* seems well supported, it does have a combination of characters not found in any extant species. The fruit *I. popensis*, in contrast, was assigned to section *Inga*, although fruits of some extant species of *Inga* assigned to section *Pseudinga* resemble *I. popensis* in having strong ribs. Assuming that both fossil organs are from the same plant, taxonomic placement for both in section *Pseudinga* is favored.

DISCUSSION

Inga has been used to exemplify the expansion of the Neotropical flora from South to North America, and the timing for this process is proposed to have started ca. 7 Ma. If this is accepted, identifications of the North American fossils assigned to this genus need to be reviewed (e.g., Richardson et al., 2001). Acceptance of isolated organs of fossil plants as representatives of extant taxa may be questionable, though many identifications of Cenozoic taxa based on isolated organs with extant relationships have been confirmed as additional organs have been discovered and more complete fossil plants have been assembled. The leaves described here are important because now two organs from the same locality assigned to *Inga* produce a strengthened argument for the presence of the genus in the La Carroza Formation ca. 50 Ma and prior to the Great American Biotic Interchange.

Further evidence supporting the presence of *Inga* in the Paleogene of North America is the fact that in the Los Ahuehuetes locality of the Coatzingo Formation (32 Ma) in Puebla, Mexico, a compound leaf with winged rachis and nectaries and a strongly ribbed fruit type has been identified as *Inga* (Fig. 1B). Other support for the presence of *Inga*, or the tribe Ingeae, in Mexico before the Great American Biotic Interchange is diversification of the tribe in Eocene–Miocene time, as represented by fruits of *Lysiloma* Benth. and fruits and leaves of *Pithecellobium* Mart., both genera from the Oligocene La Carroza Formation. Also, an inflorescence comparable to *Chloroleucon* (Benth.) Britton & Rose or *Leucochloron* Barneby & J. W. Grimes,

of tribe Ingeae, currently is being described from the Miocene amber of the Ixtapa Formation.

Graham's idea that the origin of the Mexican flora was more complicated than a simple exchange of taxa once the Panama Isthmus was established is well exemplified by *Inga*. The presence of *Inga*, as well as that of other members of the tribe Ingeae, suggests that North America was an important contributor to the Neotropical flora. Other examples further support this hypothesis. For example, Neotropical taxa like *Tapirira* Aubl., *Loxopterygium* Hook. f., and *Haplorhus* Engl. (Anacardiaceae) are well known from Eocene and Oligocene deposits of Mexico, but *Loxopterygium* is also known from Late Miocene sediments from Ecuador (Burnham & Carranco, 2004), while the other two genera are not known as fossils in South America. The spatial and temporal distribution of these Neotropical taxa highlight that the flora history cannot be explained based on a handful of examples, suggesting that further studies using both fossil and extant plants will produce a better hypothesis on the origin of modern communities.

The integration of species into communities has been a common process through geologic time, and communities changed as plants responded to a dynamic Earth. The history of flowering plants is a great example of this vigorous interaction between Earth and life processes. Both extant and fossil plants are important sources of information to support hypotheses on the development and establishment of modern communities during the Cenozoic. Recently, the origin and distribution of biomes have been used to explain the timing and expansion of vegetation types. The Neotropical flora is hypothesized to have developed under hot and humid conditions. As climate changed to drier conditions, the Neotropical flora contracted, leaving elements to face extinction or ecologically adjust and become incorporated into the newly developing biota.

Along the coasts of Mexico the Neotropical flora is well established today. However, the area occupied by this flora in Mexico is also an important region where processes of physiographic evolution due to geological activity may be explored, either at a single point in time or through intervals of time. Furthermore, the area is of interest because taxa with different geographic origins converged in this area. With this background and based on the proposed geographic affinities of the extant plants from Mexico, a hypothesis suggesting that vegetation in the area responded to the confluence of a Nearctic and a Neotropical flora became popular. Discussion of the timing of arrival and to some point the source area of the different plants of this region keeps this hypothesis under active investigation.

Inga-like leaves, fruits, and woods have been reported from Eocene and earlier sediments of the U.S.A. and Central and South America (Berry, 1924; Graham, 1992a, 1992b; Gros, 1992; Herendeen, 1992). Many reports have not been accepted and are in need of review. If *Inga* grew in the Eocene of North America, it most probably formed part of a tropical to warm temperate flora, which is known to have expanded its distribution through the Paleogene. This implies that *Inga* formed part of communities that lived under warm and humid conditions, most probably similar to a rainforest. *Inga* reached Mexico as an element of this flora, but at a time in which climatic conditions worldwide were changing, and geologic activity in northeastern Mexico was affecting sea retreatment and mountain elevation processes which, in turn, was affecting distribution of humidity (e.g., Ramírez & Cevallos-Ferriz, 2002; Calvillo-Canadell & Cevallos-Ferriz, 2005; Cevallos-Ferriz et al., 2012). It can be hypothesized that the original vegetation became fragmented as the physiography of the area was altered through geologic processes, and selective survival of the plants in the area initiated the differentiation of communities; in this case at least one zone remained hot and humid, supporting rainforest-like vegetation, while other areas were warm and dry, supporting deciduous vegetation.

Plants recently described from the La Carroza Formation suggest that this scenario is possible. They suggest that either the source community had a mixture of plants that evolved into different communities or that in the sedimentary basin plants from different sources were preserved. Since in the Carroza Formation different sediments (coarse vs. fine limonite) can be linked with distinctive leaf types, the second option seems more feasible. Perhaps the drier site contained elements like *Inga, Senna* Mill., *Chamaecrista* Moench (Fabaceae), *Lannea* A. Rich. (Anacardiaceae), and *Bursera* (Burseraceae) (Calvillo-Canadell & Cevallos-Ferriz, 2005; Rodríguez-Reyes, 2009), while the humid community contributed to the fossil assemblage members of *Populus* L., *Pleuranthodendron* L. O. Williams, *Hasseltia* Kunth (Salicaceae), *Melochia* L., *Ayenia* L., *Hibiscus* L. (Malvaceae), *Buchanania* Spreng. (Anacardiaceae), and *Cinnamomum* Schaeff. (Lauraceae) (Pérez-Maussan, 2013). Geological evolution may have led the biological processes, an idea that is strongly supported by the evolution of biomes where physical and biological processes interact to produce particular communities through time (e.g., Cevallos-Ferriz et al., 2012; Graham, 2012).

Similar processes of radiation of taxa and communities in Central and Southern Mexico were increased in the Oligocene and continued into the Miocene (e.g., Magallón-Puebla & Cevallos-Ferriz, 1994b; Ramírez & Cevallos-Ferriz, 2002; Calvillo-Canadell & Cevallos-Ferriz, 2005). The source vegetation is likely to be found in the evergreen or the deciduous vegetation differentiated earlier in the Eocene. Through the Neogene new species of lineages like *Inga*, known from older rocks, are documented, and their presence is explained due to their expansion into areas with different climates on both sides of the Sierra Madre Oriental and south of the Mexican Transvolcanic Belt, areas rising at a time when the Gulf of Mexico was also acquiring its final configuration.

Fossil floras of the central part of Mexico suggest they developed under hot and dry conditions, where physiography and climate facilitated the development of chaparrals and dry deciduous-like forest where *Inga popensis* became an important element (e.g., Magallón-Puebla & Cevallos-Ferriz, 1994b; Ramírez & Cevallos-Ferriz, 2002; Calvillo-Canadell & Cevallos-Ferriz, 2005). In contrast, fossil plants collected in areas along the gulf coast and in low-lying sites suggest the prevalence of hot and humid conditions where evergreen- and semideciduous-like forests thrived (Castañeda Posadas, 2007). In transitional areas and at mid altitudes, mesophyll forests also have been recognized, especially since Late Miocene time (Velasco-de León et al., 2010).

Geological and paleobotanical evidence suggest that Mexico fits the requirements proposed by the biome hypothesis for the expansion of Neotropical vegetation (Schrire et al., 2005; Pennington et al., 2006; Cevallos-Ferriz et al., 2012; Graham, 2012). However, local to regional climatic and physiographic conditions in North America, as Graham proposed many years ago, suggest that the history of the Neotropical Flora is more complicated than just its expansion from the Southern Hemisphere. Other taxa, not mentioned above, that can be used to support this idea are *Ruprechtia* C. A. Mey. (Polygonaceae), *Ficus* L. and *Maclura* Nutt. (Moraceae), and *Prioria* Griseb. (Fabaceae), all known from central Mexico since at least the Late Oligocene (Martínez-Cabrera, 2002; Sainz-Reséndiz, 2011).

The presence of *Inga*, and other plants that can be linked with the Neotropical flora, in Cenozoic deposits of Mexico documents further that the integration of the extant Mexican vegetation is perhaps even more complex than previously hypothesized. The record invites researchers to approach the problem in a holistic way, as emphasized by Graham (2010) and exemplified by the fossil record of *Inga*.

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CHAPTER 3

CATAHOULEA GRAHAMII, A NEW GENUS AND SPECIES OF FAGACEOUS INVOLUCRES FROM THE OLIGOCENE CATAHOULA FORMATION, EAST TEXAS, AND THE MIDDLE EOCENE CLAIBORNE FORMATION OF KENTUCKY AND TENNESSEE, U.S.A.

Melanie L. DeVore, Kathleen B. Pigg, David L. Dilcher, and Deborah Freile*

ABSTRACT

Catahoulea grahamii DeVore, Pigg, Dilcher & Freile (Fagaceae), a small, spinose involucre containing nutlets of presumed fagaceous affinity, is described herein from the Oligocene Catahoula Formation from near Huntsville, Texas, U.S.A., and the Middle Eocene Claiborne Formation of Tennessee and Kentucky, U.S.A. Involucres are (5.5–)6.5–8(–10) × 13 mm and shield-shaped with a deeply cordate base and pointed apex. The involucre is apparently 2-valved and has a fibrous body, with individual fibers splaying out in areas of poor preservation. The best preserved specimen contains three globose to ovoid nutlets, with the larger central nutlet (ca. 3 × 2 mm) flanked on either side by smaller ones ca. 1 mm wide. One specimen shows an ovule attached to a central septum. Four or five parallel veins run lengthwise along the central body and branch laterally where the involucre extends into a prominent flange. The flange thins toward the margin and is densely covered with branching spines. Peduncles are up to 9.5 × 0.3 mm, sometimes curved, and are covered with trichomes of two sizes. The organization of these specimens suggests affinities with Fagaceae. *Catahoulea* DeVore, Pigg, Dilcher & Freile occurs in the Catahoula Formation in a flora rich in transitional oaks and other Fagaceae, Juglandaceae, legumes, and palms. It is rare in the Claiborne Formation, a more diverse flora that also contains these same elements. This distribution illustrates the floristic continuity within fossil floras of the Mississippi Embayment and suggests that some Claiborne plants may have migrated westward along the Gulf Coast.

Key words: castaneoid, Fagaceae, involucre, Mississippian Embayment.

Fossil plants of the Catahoula Formation of east Texas, from an outcrop near Huntsville, in Walker County, were first described in the late 1970s (Crepet & Daghlian, 1980; Daghlian et al., 1980). This flora was found to be rich in legumes and early, transitional oaks, and also included juglandaceous fruits and more widely distributed sabaloid palms and other plants (Daghlian et al., 1980). In the following years several taxonomic papers on the plants from this outcrop provided

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important information about the early evolution of Fagaceae, including pistillate flowers and staminate catkins of intermediate, trigonobalanoid oaks occurring side by side with modern-appearing black oak leaves and white oak acorns (Daghlian & Crepet, 1983; Crepet, 1989; Crepet & Nixon, 1989a, 1989b; Borgardt & Pigg, 1999). Significant legumes were also documented from this flora (Herendeen & Dilcher, 1990, 1991; Herendeen et al., 1992). Together, these megafossil elements were interpreted as representing a dry, more seasonal climate that emerged in the Gulf Coast during the mid-Tertiary (Graham, 1999).

Included in the Oligocene Catahoula flora are several fagaceous fossil remains that are also found in the Middle Eocene Claiborne Formation of western Kentucky and Tennessee. Along with fagaceous leaves is a small, husk-like involucre containing a single large and two small nutlets. Involucres are also known from two additional specimens in the Claiborne Formation, one from the Lamkin clay pit in western Kentucky, and the other from the Warman clay pit in western Tennessee.

In this paper we describe these small, spinose involucres as *Catahoulea grahamii* DeVore, Pigg, Dilcher & Freile and discuss their affinities to genera of Fagaceae and their phylogenetic position within the family. The presence of this plant documents one of a suite of taxa shared between the Claiborne and Catahoula formations. *Catahoulea* DeVore, Pigg, Dilcher & Freile adds yet another taxon to the diverse assemblage of fagaceous plants in the Catahoula Formation, underscoring the significance of this flora to understanding diversification of the family.

MATERIALS AND METHODS

THE CATAHOULA FORMATION SITE

Crepet and Daghlian (1980) refer to the Catahoula locality as a "gravel pit of the Riverside Crushed Stone Company, 7 miles [11.3 km] north of Huntsville, TX." The locality is no longer available (DeVore & Pigg, 2010); however, we collected material in a similar matrix from an adjacent area in 2004 that contained numerous fagaceous leaves and other plant remains. Specimens in the current study were collected in 1978 by C. P. Daghlian and T. Delevoryas. They are preserved in a siliceous siltstone and bear small fragments of cuticle. Stratigraphically, the site occurs within the Catahoula Formation and is considered Oligocene in age (Galloway, 1977; Daghlian et al., 1980; Crepet & Nixon 1989a).

As to its depositional setting, the Catahoula Formation has been described as a primarily terrigenous, fluvial, deltaic, marginal marine unit (Galloway, 1977). Molluscan fossils belonging to *Amblemoidea* (Unios) suggest brackish water conditions. The presence of glauconite is an indication of shelf (60–550 m) or shallow marine environments and/or a transgressive episode. The Late Oligocene was a time of transgression after a period of lowest (–200 to –350 m relative to the present) sea level.

The outcrops of the Catahoula Formation in the region are not exposed in a way that enables us to interpret the depositional environment based on a stratigraphic context. For this reason a sedimentological analysis of the matrix of material from adjacent sites was performed, to help us better understand the source rock and its provenance (Freile et al., 2003). Petrographic thin sections of specimens preserved in the Catahoula Formation show well-preserved plant fragments, some with clear indications of permineralization. The plant fragments show primarily a reddish brown low-grade thermal maturation. Authigenic feldspar crystals, some within the organic fragments, are clearly visible. The rock samples are either finely parallel-laminated, very fine to fine-grained, angular to subangular, and moderately sorted arkoses or wavy-laminated, fine to medium-grained, subangular to subrounded, and moderately to well-sorted arkoses.

The formation contains 60% pyroclastic materials, 20%–30% arkosic sandstones, 10%–20%

argillaceous clay and minor amounts of conglomerate (Sellards et al., 1932). Accessory minerals include feldspars exhibiting good twinning, altered micas, zeolites, and nascent stage glauconitic globules. Some specimens show cementation by opal and clays, probably related to the diagenesis of volcanic ashes into silica and smectite (Freile et al., 2003).

The highly variable lithology of the samples indicates the potential of a multiple-provenance rock. Some grains are clearly volcanic in origin (including clear examples of volcanic glass clasts), others are clearly detrital (principally subrounded quartz and chert grains), while a few others are quartz grains that show the characteristic undulose extinction patterns of metamorphic quartz (Freile et al., 2003).

THE CLAIBORNE FORMATION SITES

Two specimens were also recovered from the Middle Eocene Claiborne Formation: one from the Warman clay pit of Weakly County, western Tennessee (Crepet & Dilcher, 1977), the second from the Lamkin clay pit, Graves County, western Kentucky (Dilcher & Lott, 2005). These fossils occur in a very soft claystone that often preserves cuticle well (Dilcher, 1963, 1971; DeVore & Pigg, 2010). These two clay pits have been well collected and are the source of many, if not most, of the plant remains described from the Claiborne Formation. Information about the sites is reviewed by Dilcher and Lott (2005) and Wang et al. (2013).

Specimens were removed from the matrix with fine needles. Cuticle was recovered with peels of the surfaces; however, we were not successful in obtaining sufficient material to describe details with certainty. Some information about involucre anatomy was obtained from fragments of one specimen that were mounted on a stub, sputter-coated, and studied with scanning electron microscopy (SEM) using a Hitachi S-415A SEM. Specimens are housed at the Florida Museum of Natural History, Gainesville (UF).

SYSTEMATICS

Family: Fagaceae

Genus: ***Cataboulea*** DeVore, Pigg, Dilcher & Freile, gen. nov.

Generic diagnosis: Small, spinose involucres with fibrous bodies, shield-shaped with a deeply cordate base and pointed apex; involucre enclosing up to three ovoid nutlets; central nutlet larger, flanked by 2 smaller nutlets; ovule attached to a central septum in apical portion of the larger nutlet; central body of involucre with 4 or 5 major parallel veins that branch laterally, periphery of involucre expanded into a prominent flange; flange densely covered with helically arranged, branched spines. Peduncle long, covered with two sizes of trichomes.

Species: ***Cataboulea grahamii*** DeVore, Pigg, Dilcher & Freile, sp. nov.

Holotype: designated here: UF 15841-28768 (Figs. 1A, 2A, B, D, E).

Paratypes: designated here: UF 15841-29214 and 29214′ (Fig. 1B, C); UF 15841-29213 (Fig. 1H); UF 15841-7948 (Fig. 1I); UF 15841-11780 (Fig. 1D); UF 15841-29205 and 29205′ (Fig. 1G); UF 15841-31384 (Fig. 1F); UF 15841-11782 (Fig. 1E); UF 15826-51307 (Fig. 2C); UF 15826-29215 (Fig. 2F); UF 15841-11781 (Fig. 2G); UF 15841-29209 and 20209′ (Fig. 2H). Not figured: UF 15841-11783; UF 15841-28767 and 28676′; UF 15841-29207; UF 15841-29210; UF 15841-29211 and 29211′; UF 15841-29217; UF 15815-5347; UF 25825-5347; UF 15826-29215; UF 15841-x; and UF 15841-29212.

Stratigraphy and age: The holotype and 18 paratype specimens are from the Oligocene Catahoula Formation (Figs. 1A–I, 2A, B, D, E, G, H).

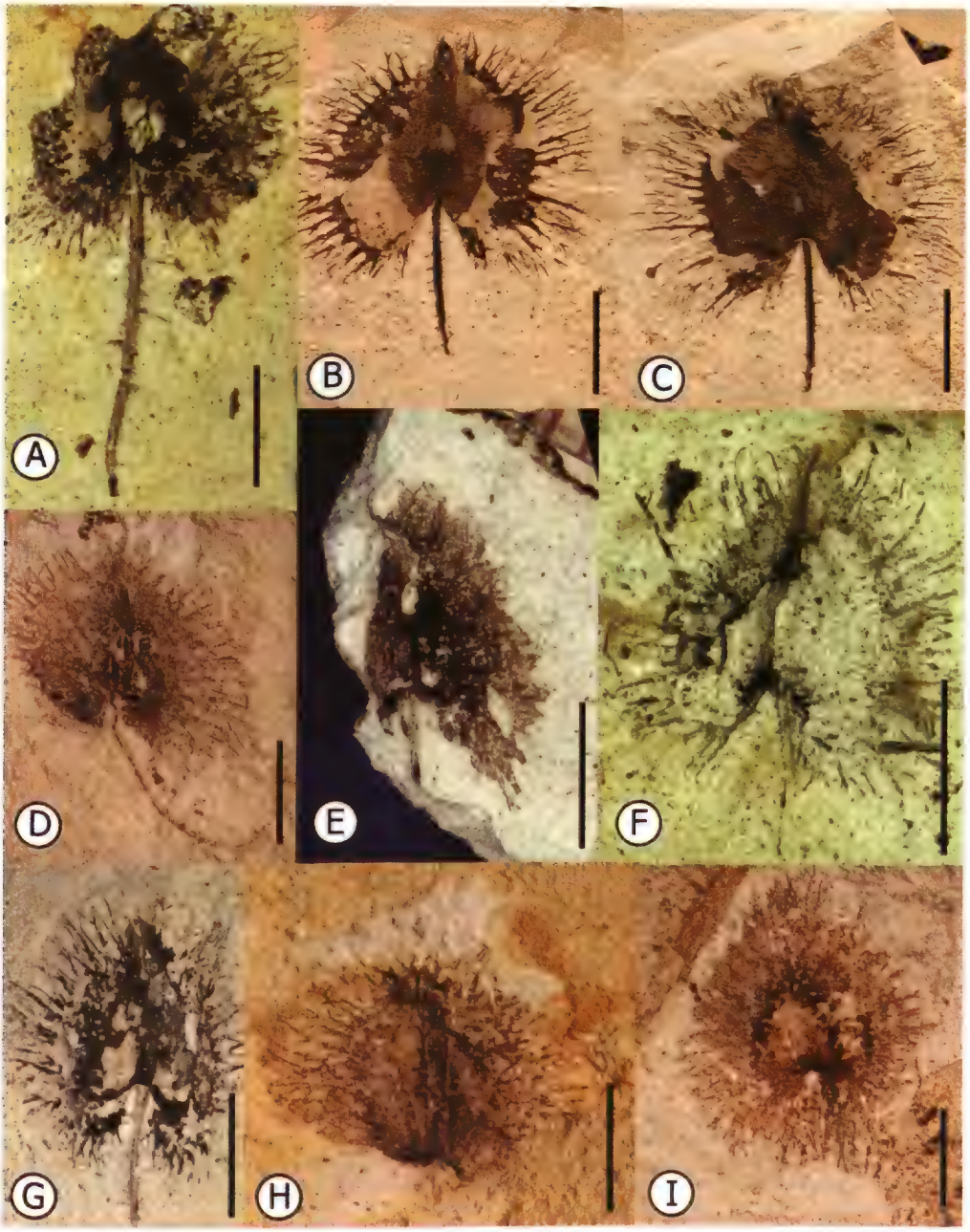

FIGURE 1. *Catahoulea grahamii* DeVore, Pigg, Dilcher & Freile. —A. Holotype specimen showing nutlet containing seed (UF 15841-028768). B, C. Part (B) and counterpart (C) of involucre. —B. Involucre part (UF 15841-29214). —C. Counterpart of B (UF 15841-29214′). —D. Involucre with curved peduncle (UF 15841-11780). —E. Specimen compressed in minor plane (UF 15841-11782). —F. Specimen showing prominent branched spines (UF 15841-31384). —G. Specimen compressed in minor plane (UF 15841-29205′). —H. Specimen showing venation (UF 15871-29213). —I. Specimen showing one nutlet (UF 15841-11781). Scale bar = 1 mm.

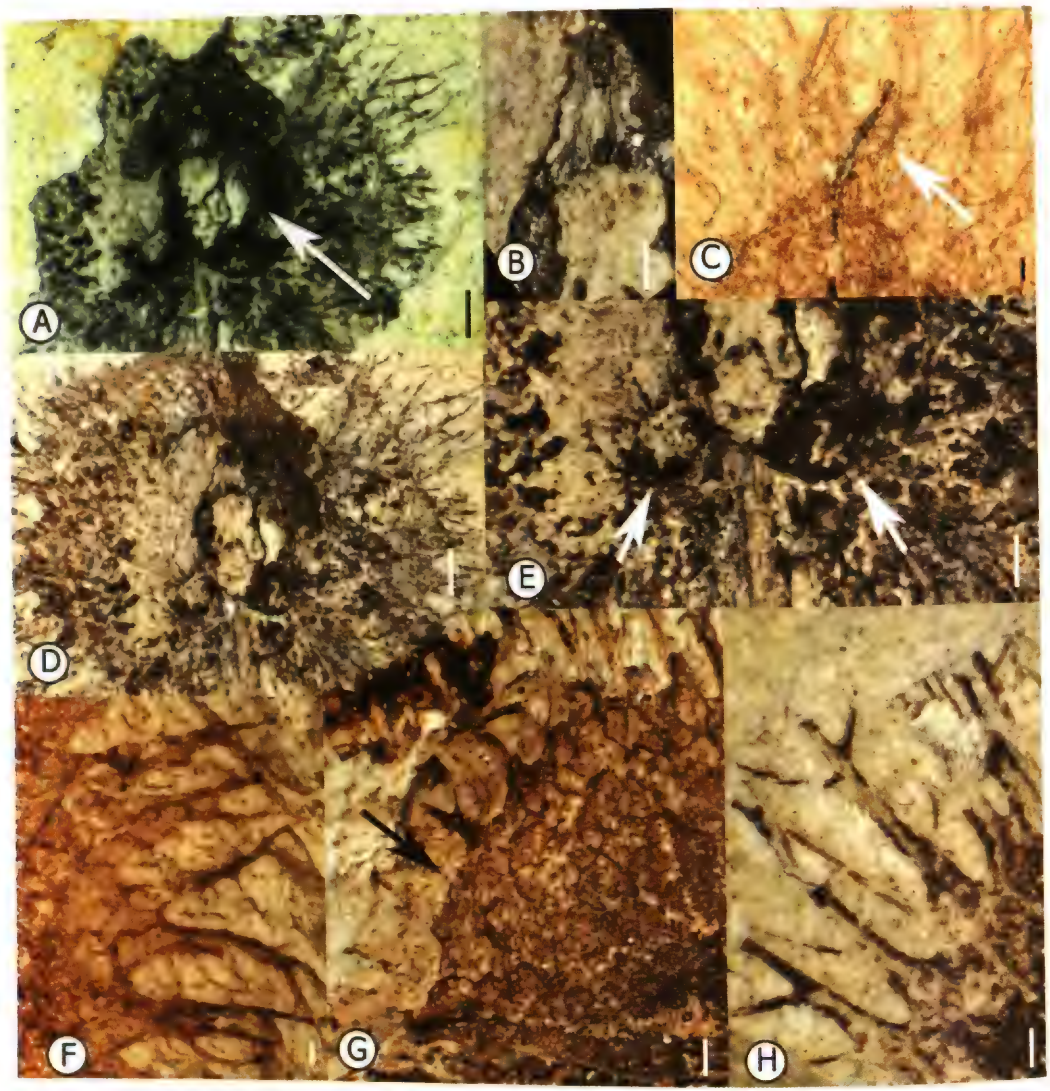

FIGURE 2. *Catahoulea grahamii* DeVore, Pigg, Dilcher & Freile. —A. Detail of holotype showing large central nutlet (at arrow) containing seed attached to septum (UF 15841-028768). —B. Detail of holotype showing base of style. —C. Style (at arrow) (UF 15826-51307). —D. Detail of holotype specimen at same magnificaton as A, after removal of surrounding matrix. —E. Detail of holotype showing part of large nutlet and positions of two smaller nutlets (at arrows). —F. Detail of branched spines at margin of involucre (UF 15826-29215). —G. Detail showing two involucral bracts (arrow). —H. Detail of involucral spines (UF 15841-21909). Scale bar = 0.1 mm.

Three additional specimens come from the Middle Eocene Claiborne Formation, one from the Lamkin clay pit, western Kentucky, and two from the Warman clay pit, western Tennessee (Fig. 2C, F).

Etymology: The genus name *Catahoulea* refers to the Catahoula Formation of east Texas, which is the source of the fossil material. The epithet *grahamii* honors native Texan Alan K. Graham for

his many contributions to Tertiary paleobotany and palynology.

Species diagnosis: Involucres (5.5–)6.5–8(–10) mm long, up to 13 mm wide, central nutlet ca. 3 × 2 mm, globose to ovoid, flanked by two nutlets ca. 1 mm wide. Spines helically arranged, branched. Peduncle up to 9.5 × 0.3 mm, covered with trichomes ca. 1 mm long, mixed with much shorter ones.

Description: The description of *Catahoulea* is based on 22 specimens of partial involucres, 18 of which are from the Catahoula Formation and three from the Claiborne Formation (Figs. 1, 2). Involucres are (5.5–)6.5–8(–10) mm long and up to 13 mm wide. The involucre has a fibrous body; it is shield-shaped with a deeply cordate base (Fig. 1A–C, F, G) and a pointed apex (Fig. 1B, D, F, G, I), with individual fibers splaying out in areas of poor preservation. The involucre appears to split in half along its long axis, as evidenced by the overlapping flanges at the periphery of the involucre (Fig. 2G), and the details of part-counterpart specimens (e.g., Fig. 1B, C).

In the best-preserved specimen three ovoid nutlets are found (Fig. 2A, D, E), with the central nutlet ca. 3 × 2 mm (Fig. 2A). It is flanked on either side by smaller nutlets ca. 1 mm wide (Fig. 2D, E). This specimen also shows an ovule within the larger nutlet attached to a central septum near the nutlet apex (Fig. 2A, D, E). In a second specimen the large central nutlet is visible (Fig. 1I). In a part-counterpart specimen the involucre is still intact, and the nutlets are more difficult to discern because they are partly obscured by the involucre valves surrounding them (Fig. 1B, C). Several specimens show a style protruding above the involucre (Fig. 2B, C).

The central body of the involucre seen in its major plane shows venation with 4 or 5 prominent, vertically oriented veins that branch laterally (Fig. 1D, H). At the periphery, the involucre has a prominent thin flange that is densely covered with helically arranged, branched spines (Figs. 1A–I, 2A, C, D, F–H). Involucres are pedunculate with peduncles up to 9.5 mm × 0.3 mm, sometimes curved (Fig. 1A–G), and covered with trichomes of two sizes, the larger ones ca. 1 mm long and the smaller ones much shorter (Fig. 1A–G).

DISCUSSION

FAGACEOUS AFFINITIES OF *CATAHOULEA*

Catahoulea can be assigned to Fagaceae on the basis of its general morphological structure, including a valvate involucre with a dichasial arrangement of nutlets within the involucre, and a characteristic fagaceous morphology and distribution of branched spines. Although *Catahoulea* shares a variety of morphological features with several known members of Fagaceae, its combination of features is not identical to any currently recognized extant or fossil form, and it can be therefore recognized as a distinct genus.

Catahoulea may bear some superficial resemblance to the spinose involucres known within Betulaceae subfamily Coryloideae, particularly those in some species of *Corylus* L. and in the extinct Paleogene *Palaeocarpinus* Crane (Pigg et al., 2003). However, the spinose involucres of *Catahoulea* differ significantly in several ways. The first feature that differs is the general morphology of the involucre. Although involucres of Fagaceae vary in morphology, number of valves (number of fruits from 3 to a reduction of 1), and general organization, they all have a similar structure, with a relatively thickened outer region lined with a thin inner, often sclerenchymatous layer, adjacent to the nutlet (Brett, 1964).

A well-known trend of reduction occurs within involucres of Fagaceae from 3-fruited to single-fruited forms (Forman, 1966; Manos et al., 2008). Nevertheless, involucres of Fagaceae all have a similar structure, with a relatively thickened outer region lined with a thin inner, often sclerenchymatous layer, adjacent to the nutlet (Brett, 1964).

In contrast, Coryloideae species have pairs of more or less equally sized bracts with spiny to entire margins that each bear a single nutlet (Pigg et al., 2003). The paired involucre bracts in Coryloideae are leaflike and much thinner than in *Catahoulea*. Furthermore, the bract is fused over the basal portion of the nut and a circular scar comprised of the vascular bundle endings is clearly visible on the nut when it is detached (Manchester et al., 2004). In *Ostrya* Scop., the involucre is utricate and encloses the nutlet (Manchester & Crane, 1987).Variations within Coryloideae occur, with these leafy structures bearing nutlets in pairs (*Corylus*, *Carpinus* L., Paleocene species of *Palaeocarpinus*) or clustered (e.g., *Ostrya*). Two extinct coryloid genera, the Paleocene *Cranea* Manchester & Chen (Manchester & Chen, 1998) and the Oligocene *Asterocarpinus* Manchester & Crane (Manchester & Crane, 1987) have additional variations of leafy involucres. In *Cranea* the winglike bracts remain attached to the infructescence axis, and the nutlets are shed. *Cranea* has similarities to *Ostryopsis* Decne., which has no known fossil record. *Asterocarpinus* has an involucre with 4 to 6 radiating winglike arms (Manchester et al., 2004). Both genera, like others of Coryloideae, are decidedly unlike *Catahoulea*.

A second feature that differs between the Fagaceae and Betulaceae is the morphology and distribution of the spines. In Fagaceae they vary from being stalked and branched in *Chrysolepis* Hjelmq. to variable in *Castanopsis* (D. Don) Spach (sessile spines, conical spines, transverse ridges, and scales), to irregularly branched, often interlocking spines in *Castanea* Mill. (Forman, 1966). Despite these differences, spines in Fagaceae are characteristically dichotomously branched with all the subsidiary spines oriented on the inner side of the involucre (Forman, 1966). The involucre bracts are vascularized by primary veins radiating from the base, distally forking, and then sometimes leading into the marginal spines. *Catahoulea* has branched spines that are perhaps most similar to *Chrysolepis* (Figs. 1A–I, 2G).

In contrast, in Betulaceae spines are more randomly arranged and extend at various irregular angles from the involucre. In *Corylus*, spines come straight out from their points of origin and branch pinnately. In *Palaeocarpinus*, adjacent primary veins are connected by a network of reticular elongate areoles formed by the secondaries and tertiaries (e.g., *P. barksdaleae* Pigg, Manchester & Wehr, Pigg et al., 2003); or they can be deeply dissected and appear bipinnate and spinose (e.g., *P. dakotense* Manchester, Pigg & Crane, Manchester et al., 2004). Forman (1966) discusses the developmental origin of these spines in extant Fagaceae from arcs of meristematic tissue, resulting in a regular, helical arrangement that contrasts with the more random arrangement of spines on coryloid involucres. Families other than Betulaceae that also produce winged involucre bracts (e.g., Nothofagaceae) do not appear to have any obvious similarities to *Catahoulea*.

THE FOSSIL RECORD OF FAGACEAE

The fossil record of Fagaceae is extensive, and it has been reviewed in detail elsewhere (Crepet, 1989; Nixon & Crepet, 1989; Friis et al., 2011). Occurrences of fagaceous leaves are common throughout the Tertiary; however, there are considerable difficulties in relating them directly to modern genera (Jones, 1986; Jones & Dilcher, 1988; Gandolfo, 1996). Pollen has been useful in demonstrating the presence at the family level, and sometimes at the infrageneric level (e.g., Crepet & Daghlian, 1980); wood can be identified to family and, in some instances, to genus (Wheeler & Manchester, 2002; InsideWood, 2004 onwards). However, when recognizing Fagaceae in the fossil record, the most confident determinations are made based on reproductive structures.

In the context of extant genera, *Fagus* L. is known from cupules, nutlets, and leaves in the latest Early Eocene to earliest Middle Eocene floras of the Okanogan Highlands at McAbee, British Columbia, Canada, and Republic, Wash-

ington, sites (Manchester & Dillhoff, 2004). The earliest evidence for *Castanea* is reproductive structures in the Middle Eocene Claiborne Formation, where the genus is represented by spiny cupules and staminate inflorescences (Crepet & Daghlian, 1980). *Quercus* L. and *Castanopsis* involucres and fruits are first recognized in the Middle Eocene Clarno nut beds of central Oregon, where wood comparable to both extant *Quercus* and *Lithocarpus* Blume and extinct Fagaceae is also recognized (Manchester, 1994, 1999; Wheeler & Manchester, 2002). Reproductive structures of fossil trigonobalanoids, quite similar to extant genera as well as to modern-appearing *Quercus*, are known from the same Oligocene fossil beds as *Catahoulea* (Daghlian & Crepet, 1983; Crepet & Nixon,1989b; Nixon & Crepet, 1989; Borgardt & Pigg, 1999).

Extinct genera most pertinent to comparison with *Catahoulea* are the Tertiary forms *Fagopsis* (Lesquereux) Cockerell (Manchester & Crane, 1983), *Pseudofagus* Smiley & Huggins (Smiley & Huggins, 1981) and, perhaps most significantly, *Cascadiacarpa* Mindell, Stockey & Beard (Mindell et al., 2007). *Fagopsis* produces leaves with an uncanny resemblance to modern *Fagus*, and the two genera are now known to have grown together in floras of the Okanogan Highlands (Manchester & Dillhoff, 2004). Unlike the characteristic nutlets in the spiny involucre of *Fagus*, however, mericarps of *Fagopsis* were borne initially as a ring that breaks up on dispersal into wedge-shaped fruits (Manchester & Crane, 1983). This taxon is widespread in western North America in Eocene floras, including those of the Okanogan Highlands and Florissant (Manchester & Crane, 1983).

Pseudofagus is known from the Clarkia and Emerard Creek floras of the Miocene of Idaho (Smiley & Huggins, 1981). It has beech-like leaves attached to yet another unusual fruit type, a single tri-keeled nut surrounded by a branched involucre. These two genera illustrate how the discovery of leaves with fertile attachments can document taxa that would have remained unknown on the basis of separate vegetative and reproductive organs alone.

Cascadiacarpa is from the Eocene Appian Way site on Vancouver Island, British Columbia, Canada (Mindell et al., 2007). Unlike *Catahoulea*, *Cascadiacarpa* is anatomically preserved. However, there are several similarities between *Catahoulea* and *Cascadiacarpa* in the features that can be compared and also several distinct differences.

A major difference between *Catahoulea* and *Cascadiacarpa* is the presence in *Cascadiacarpa* of a single nutlet that is adnate to the involucre. *Catahoulea* involucres contain three nutlets, one central large one and two lateral smaller ones, and there is no evidence of fusion between nutlets and involucre. Furthermore, the spines in *Cascadiacarpa* are arranged irregularly, an unusual feature for Fagaceae, which typically produce spines in distinct series of concentric or helical rows (Forman, 1966). The two fossil types can be regarded as separate, extinct genera.

PHYLOGENETIC RELATIONSHIPS WITHIN FAGACEAE

The taxonomic distribution of spinose involucres within Fagaceae is interesting in light of new understanding of phylogenetic relationships. Spines are present in *Castanea*, *Castanopsis*, and *Chrysolepis*, genera that, along with *Lithocarpus*, were traditionally recognized as subfamily Castaneoideae (Nixon & Crepet, 1989). The scalelike structures on the involucres of fagaceous genera that lack spines (e.g., *Quercus*, *Lithocarpus*) were regarded as reduced to highly reduced and occur in taxa where nutlet number and valve number are also reduced to one.

In the most recent generic-level treatment of Fagaceae, and phylogenetic analysis based on nuclear and chloroplast DNA variation of the family, a new monotypic genus, *Notholithocarpus* Manos, Cannon & S. H. Oh, is recognized for the previously named *Lithocarpus densiflorus* (Hook. & Arn.) Rehder (Manos et al., 2008). Within this context, support exists for recognizing

the castaneoids as two lineages derived from the *Colombobalanus–Formanodendron–Trigonobalanus* clade: (1) *Chrysolepsis* + *Lithocarpus* and (2) *Castanea* + *Castanopsis* + *Notholithocarpus* + *Quercus*. Spinulose cupules have apparently evolved independently within each lineage, and therefore twice within the Fagaceae (Manos et al., 2008; Oh & Manos, 2008).

The reduction, by the loss of lateral flowers or second-order branches in the dichasium, to the single-fruited condition has apparently occurred at least four times within modern genera (*Castanea*, *Castanopsis*, *Lithocarpus*, and *Notholithocarpus* + *Quercus*), or five times if the latter two genera do not share a common single-fruited ancestor.

Catahoulea is characterized by an involucre type unlike any found among extant members of Fagaceae. The shield-shaped, paired valves expanding into a thin flange with distally helically arranged spines is unique. It appears that *Catahoulea* represents yet another lineage within the Fagaceae stemming from the *Fagus-Triganobalanus* base of the family. Clearly, the Eocene and Oligocene is a time frame in which the crown group for the Fagaceae experienced a radiation, leading to modern taxa within the family. What is intriguing in the case of *Catahoulea* is that this fossil genus is derived within an extinct lineage. In essence, it represents the last of yet another lineage within the castaneoid genera.

DISTRIBUTION OF FAGACEAE IN EASTERN VERSUS WESTERN NORTH AMERICA

The co-occurrence of *Catahoulea* in an Oligocene flora of east central Texas, along with a rare occurrence at two Middle Eocene sites in the Claiborne Formation, underscores the relationship between these floras. *Catahoulea* is not particularly common. In the Oligocene flora in Texas all 19 specimens come from a single locality. In the well-known Claiborne Formation, it has been recognized only three times among the thousands of fossils collected and the many taxa described. *Catahoulea* co-occurs at both sites with other fagaceous elements, including transitional oaks, *Castanea*, and, at the Oligocene site, with apparently modern *Quercus* (Manchester, 1999). Along with Fagaceae, several types of legumes are important elements of both floras.

In contrast to what we know currently of the Catahoula flora, the Claiborne flora appears to be considerably more diverse throughout its distribution at many sites (Dilcher & Lott, 2005). Most notably present in the Claiborne, and yet apparently absent in the Catahoula flora, are hallmarks of megathermal floras such as Lauraceae. Floristic change in floras of the Mississippi Embayment are gradual and transitional in their nature, in large part because of their deposition on a passive margin (DeVore & Pigg, 2010), in contrast to the western North American Tertiary floras that were deposited in tectonically active volcanic sites.

The castaneoid elements of the Mississippian Embayment are distinct from *Chrysolepsis* and *Notholithocarpus*. Both of these endemics to the California Floristic Province are highly divergent members of two different major Fagaceae lineages and have been interpreted as remnants of a broadleaf evergreen flora that persists today in Indonesia (Manos et al., 2008). Tiffney and Manchester (2001) suggested that dispersal of these evergreen forests was through the Northern Hemisphere via the Bering and North Atlantic land bridges. In the case of the castaneoids, and the differences between those in the Mississippian Embayment and their apparent distinctness from paleoendemics of western North America, we hypothesize that thermophilic taxa in Fagaceae possibly migrated along Atlantic embayments into eastern North America, while those in the West dispersed along the Pacific Coast.

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AN EXTINCT CAESALPINOID FLOWER FROM THE EOCENE OF WESTERN TENNESSEE

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ABSTRACT

Fabaceae has an abundant and diverse fossil record from the Eocene of southeastern North America, where all three of its subfamilies have been reported based primarily on pollen, fruits, and leaflets, and occasional flowers. Here, we document the presence of a flower within the tribe Detarieae s.l., from the Dawson pit, Middle Eocene Claiborne Group of western Tennessee. The fossil was collected from clay in a drying bin of the Spinks Clay Company, which came from the Dawson pit, three miles west of Huntington, Tennessee. The fossil-bearing lithofacies is dark to light gray (with fine striations) to black organic-rich clay. Analyses of floral morphology and palynological characters were performed under transmitted light microscopy and SEM microscopy. This specimen displays a number of characters within the family Fabaceae, subfamily Caesalpinioideae, tribes Cassieae and Detarieae s.l. These characters include bracteoles subtending a zygomorphic flower with four stamens and a stipitate gynoecium adnate to the side of a hypanthium. The specimen has well-developed bracteoles, a character that distinguishes Detarieae s.l. from other tribes in the Caesalpinioideae. A new fossil genus and species, *Eocaesalpinia herendeenii* Dilcher, Lott, Gibson & Dudley, is herein established based on a unique set of floral features for Detarieae s.l., thus extending the history of this tribe back to the Eocene clays of Tennessee.

Key words: Claiborne Group, flower, legume, Middle Eocene, Tennessee.

The Fabaceae have an abundant and diverse fossil record, particularly from the Eocene Claiborne Group in southeastern North America, where all three of its subfamilies, and in particular the tribes Caesalpinieae and Sophoreae, have been reported (Herendeen, 1992; Herendeen et al., 1992). The fossil record of Fabaceae is primarily based on pollen, fruits, and leaflets, and occasional flowers (Herendeen & Dilcher, 1990). Previously recognized fossil legume flowers in the Eocene of southeastern North America include the Mimoseae and Sophoreae (Crepet & Dilcher, 1977; Daghlian et al., 1980; Crepet & Taylor, 1986; Crepet & Herendeen, 1992). In this paper, we describe the fossil flower *Eocaesalpinia herendeenii* Dilcher, Lott, Gibson & Dudley and present morpholog-

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ical evidence indicating close affinity with the Detarieae s.l. (Fabaceae: Caesalpinioideae). The legume subfamily Caesalpinioideae is well represented in the same geologic horizon (Claiborne Group; Berry, 1916, 1930; Herendeen & Dilcher, 1990, 1991; Herendeen, 1992) based upon fossil leaflets and fruits. The Detarieae consist of 82 extant genera and ca. 747 species (Mackinder, 2005) with a wide range in floral and pollen morphology. The flower is from Dawson pit, Tennessee, which has the most unique clay pit flora of over 20 floras from this area because of the abundance of small angiospermous leaves. Flowers are also quite rare for this clay pit, for out of 260 specimens collected, only one other (unidentified) flower was found.

MATERIALS AND METHODS

The fossil was collected from a drying bin that belonged to the Spinks Clay Company, which is currently owned by United Clay Company (Unimin) of Gleason, Tennessee. Each bin contains material from a single locality, in this case the Dawson pit, located three miles west of Huntington, Tennessee (UF locality no. 18903, 35°56′30″N, 88°15′10″W). Subsequent collecting in the pit yielded additional plant material and allowed us to identify the fossil-bearing interval. The fossil-bearing lithofacies is a massive bedded, dark to light gray (with fine striations) to black organic-rich clay belonging to the Middle Eocene Claiborne Group. This lithofacies is overlain by well-sorted unfossiliferous sand that is locally cross-stratified. A small channel of sand cuts into the gray clay lithofacies and is in turn cut by the overlying sand lithofacies. The Claiborne Group is exposed in a north-south trending belt on the eastern flank of the Mississippi Embayment. Regionally, the Claiborne is chiefly sand with clay lenses of limited areal extent. The Claiborne is generally interpreted as a series of oxbow lakes and sand channels of an ancient floodplain-river system (Potter & Dilcher, 1980).

The botanical affinities were determined by the study of floral morphology and palynological characters of 22 genera in Detarieae s.l. (from 82 genera; Mackinder, 2005) of Fabaceae, and three genera from Connaraceae. We restricted the search of extant affinities to genera that possess characters similar to the fossil flower (Table 1). Classification follows APG III (APG, 2009) and Polhill and Raven (1981).

Photographs were taken with a Zeiss AxioCam camera mounted on a Zeiss Axiophot transmitted light microscope, which is inline with a Zeiss AxioVs40 version 4.5 imaging software (Thornwood, New York, U.S.A.), and a Nikon Coolpix990 camera (Melville, New York, U.S.A.). SEM photographs were taken with a Hitachi S-570 system (Hitachi, Japan).

SYSTEMATICS

Order: Fabales Bromhead

Family: Fabaceae Lindl.

Subfamily: Caesalpinioideae DC.

Tribe: Detarieae DC. s.l.

Genus: ***Eocaesalpinia*** Dilcher, Lott, Gibson & Dudley, gen. nov.

Etymology: "Eo" is a prefix used in ancient times, symbolizing dawn or beginning; "caesalpinia" refers to the taxon's affinity with the subfamily Caesalpinioideae.

Generic diagnosis: Flower bisexual, superior, pedicellate, subtended by two valvate bracteoles. Sepals two; petals four, closed; stamens four, unequal; sepals, petals, and stamens all adnate to the receptacle. Anthers introrse, longitudinally dehiscent, each with four pollen sacs. Gynoecium adnate near the base and to one side of the receptacle. Ovary superior, stipitate and curved. Style

coiled. Pollen tricolpate, prolate/oblate spheroidal, exine coarse, striato-reticulate, colpi meeting at the pole, colpus membrane broken to near the base.

Species: ***Eocaesalpinia herendeenii*** Dilcher, Lott, Gibson & Dudley, sp. nov. Figure 1A–F.

Holotype: designated here: UF 18903-30741 (Fig. 1A–F).

Type locality: Dawson pit, Carroll County, Tennessee, U.S.A.

Stratigraphy and age: Lower Claiborne Group, Middle Eocene.

Etymology: The specific epithet "herendeenii" is given in honor of Patrick Herendeen for his many contributions to the fossil history of Fabaceae.

Number of Specimens Examined: One.

Repository: Paleobotany/Palynology Collections, Florida Museum of Natural History.

Specific diagnosis: Same as genus.

Description: Slightly zygomorphic bisexual flower, superior and pedicellate, pedicel straight, 4 × 1 mm; sepals, petals, and stamens adnate to the receptacle; two valvate bracteoles subtending flower, 4.8–5.2 × 1.8–2.8 mm; two incomplete sepals, ca. 4 mm long; four petals, closed, oblong, 4–5 × 2.8 mm; androecium with unequal free filaments, four stamens, two long incomplete filaments ca. 4 × 0.25 mm and attached to apical portion of the receptacle, two anthers at the base of the petals, introrse, longitudinal dehiscence, 1.25–1.5 × 0.5 mm, each with four pollen sacs; unicarpellate, gynoecium adnate near the base and to one side of the receptacle; ovary superior, stipitate, oblong and curved, 4 × 1 mm, with dorsal vascular strand; style coiled and incomplete, ca. 5.5 mm. Pollen tricolpate, prolate/oblate-spheroidal, 21.4 × 19.3–21.4 µm (Polar/Equatorial ratio = 1.11–1.0); exine coarse striato-reticulate, muri width 0.3–0.4 µm; colpi meeting at the pole, colpus membrane broken to near the base, colpus membrane width 1–2 µm.

The fossil flower is immature, incomplete, and lacks two anthers and a stigma. This limits the potential for character matches with extant taxa. The sepals and petals appear to arise from under a receptacle, but this structure is in question. It may be a central disk or a shallow hypanthium. One bracteole, which is horizontal to the axis, has an incurved shape and is considered valvate. The second bracteole is slightly reflexed and is narrower than the incurved bracteole (Fig. 1A, B). Both bracteoles are high on the pedicel, but we cannot determine if they are caducous or persistent based on a single flower. Two sepals, which are different in texture from the petals, extend out from the side and top of the closed petals (Fig. 1C). Two pairs of petals are upright and appressed to each other (Fig. 1C, D). There are two stamens with long filaments, with one long filament flanking the petals while the second long filament is distorted and overlays the pedicel, and in both the anthers are missing (Fig. 1A, C). There are two stamens with short filaments. The anthers of these stamens sit at the base of petals, with the short filaments close to the receptacle (Fig. 1C, D). Well-preserved pollen was removed from these anthers, but the colpi membrane was usually torn so it is unknown if pores are present. The pollen is striate-reticulate (Fig. 1E, F). An ovary arises from the base and to one side of the receptacle, which gives the flower a slight zygomorphic appearance. It is not clear if the gynoecium is glabrous or covered with trichomes. The style is curved and missing a stigma.

DISCUSSION

Eocaesalpinia herendeenii possesses characters such as bracteoles, a superior flower, and a single gynoecium that resembles an immature pod-like fruit.

TABLE 1. Character comparison between genera of Connaraceae and Fabaceae (Detarieae s.l.).

Family/ Group[a]	Genus	Habit/Range	Flower	Hypanthium	Bracteoles	Sepals	Petals
Fabaceae/ Amherstia	*Amherstia* Wall.	tree/Burma	zygom., bisexual	elongate	large, persistent, high on pedicel	4 (1 large), petaloid	5 (3 large, 2 minute), free
	Humboldtia Vahl	shrub-tree/ India, Ceylon	zygom., bisexual	present	small to large, free-connate, persistent, valvate, high on pedicel	4	3 or 5, clawed
Berlinia	*Isoberlinia*	tree/Africa	radial, bisexual	short	2, free, persistent, valvate	4 to 6, free, linear	5(6), median clawed
Brachystegia	*Aphanocalyx* Oliv.	tree/Africa	zygom., bisexual	short	2, valvate, sepaloid, persistent, high on pedicel	0 to 3	1(2)
	Brachystegia Benth.	tree/Africa	zygom., bisexual	short, glandular	2, valvate, sepaloid, persistent, high on pedicel	tepals 0 to 10, small	
	Cryptosepalum	herb-shrub-tree/Africa	zygom., bisexual	present	large, free, persistent, valvate, high on pedicel	0 to 6, minute	1 or 2 to 3
	Didelotia	tree/Africa	slightly zygom., bisexual	present	large, free, persistent, some valvate, high on pedicel	4 to 6, minute	1 to 4 or 5
	Monopetalanthus Harms	tree/Africa	zygom., bisexual	short	2, valvate, sepaloid, pubescent, persistent	0 to 5, large to minute, oblong, triangular, lanceolate	1 to 5 (1 large, others minute)
Brownea	*Brachycylix* (Harms) R. S. Cowan	shrub/ Colombia	zygom., bisexual	present	small, connate, persistent	4	5 (3 large, 2 small), clawed
	Brownea	tree/Tropical America, West Indies	radial, bisexual	present	connate with 2 lobes, persistent, high on pedicel	4 to 5, petaloid, imbricate	5, slightly unequal, imbricate, clawed
	Eperua Aubl.	tree/South America	zygom., bisexual	present	small, free, valvate-distant, persistent, caducous, middle of pedicel	4	1 or 2 to 5 (1 large, others small)

Stamens	Filaments	Anthers	Gynoecium	Ovary	Style	Stigma	Pollen morphology	Reference[b]
10, fertile, diadelphous	9 united, 1 free	dorsifixed, introrse	adnate	stipitate, pubescent	filiform	capitate	tricolporate, striate	3, 7–9, 14, 17
5, fertile; 5 staminoidia, unequal	free	dorsifixed	–	stipitate	filiform	–	tricolporate, reticulate, rugulose reticulate	7, 8, 13, 17
10 to 13, fertile, ± exserted, diadelphous, two whorls	free	dorsifixed, longitudinal dehiscence	central to adnate	stipitate	filiform, elongate	–	tricolporate, striate, striate-reticulate	1, 3, 7, 8, 16–17
10, fertile	free or slightly united basally	–	centrally attached	stipitate, short	filiform, oblique	–	striate	1, 3, 8, 14, 17
9 to 18, fertile, equal-unequal, with or without staminoidia	free to united	longitudinal dehiscence	centrally attached	stipitate, pubescent	–	capitate	tricolporate, coarsely reticulate	1, 3, 7, 8, 14, 17
3 to 6 or 8, fertile, with or without staminoidia	–	dorsifixed	adnate	stipitate	filiform	–	striate	3, 8, 13, 17
4 to 6, fertile, unequal, with staminoidia	free	dorsifixed, longitudinal dehiscence	centrally attached	sessile or subsessile	–	–	tricolporate, striate	7, 8, 13, 17
8 to 10, equal	9 fused at base, 1 free	dorsifixed, longitudinal dehiscence	central to adnate	stipitate, pubescent	filiform	–	striate	1, 3, 8, 9, 14
5 fertile, unequal, with staminoidia	united	dorsifixed, longitudinal dehiscence	adnate	stipitate	–	not peltate	tricolporate, striate	7, 8, 13
9 to 15	free or unequally connate	dorsifixed, introrse, longitudinal dehiscence	adnate	stipitate, pubescent	filiform	capitate	tricolporate, reticulate, striate, striate-reticulate, scabrate-punctate	3, 7, 8, 14, 17
10 or 5 to 9, fertile, equal to unequal, some staminoidia	free to united	dorsifixed, longitudinal dehiscence	–	stipitate	–	–	tricolporate, coarsely reticulate, rugulate reticulate, punctate-microreticulate, rugulate, verrucate	7, 8, 13, 17

(*continued*)

TABLE 1. (*continued*)

Family/ Group[a]	Genus	Habit/Range	Flower	Hypanthium	Bracteoles	Sepals	Petals
Crudia	*Crudia*	tree/tropical	radial, bisexual	present	small to large, free, sometimes persistent-caducous, middle of pedicel	4 or 5	0 or rarely vestigial 1 to 3
Cynometra	*Cynometra* L.	shrub-tree/ tropics	radial-zygom., bisexual	present, small disk	2, petalloid, caducous, low on pedicel	3 to 5, some reflexed, oblong to ovate	5, subequal, imbricate, oblong-lanceolate
	Schotia	herb-shrub-tree/Africa	radial-zygom., bisexual	present, sometimes lobed	2, caducous, middle of pedicel	4, imbricate, oval	5, subequal, imbricate, some clawed, ovate-oblong
Detarium	*Gilletiodendron* Vermoesen	tree/Africa	zygom., bisexual	short	small, caducous, low on pedicel	4, imbricate, subequal, reflexed, glandular	5, subequal
Hymenostegia	*Afzelia*	tree/ Africa-Asia	zygom., bisexual	present	small, free, rarely persistent-caducous, high on pedicel	4	1 or 1 to 5 (1 large & clawed, others small)
	Hymenostegia	shrub-tree/ Africa	radial-zygom., bisexual	present	2, petaloid, persistent, high on pedicel	4, imbricate, elliptic	(1)2 to 5, free
	Lysidice	shrub-tree/ Asia	zygom., bisexual	present	showy, persistent, middle of pedicel	4 to 5, imbricate, lanceolate, obovate, elliptic	5, [illegible] long-clawed, obovate
	Saraca L.	tree/Asia	radial, bisexual-unisexual	present	small to large, free, sometimes persistent, high on pedicel	4 to 6	0
Macrolobium	*Anthonotha*	tree/Africa	radial-zygom., bisexual	present	small to large, free, persistent, valvate, high on pedicel	4 to 5	2 to 6
	Gilbertiodendron	tree/Africa	zygom., bisexual	present	large, sepaloid, free, persistent, valvate, high on pedicel	4 to 5	5 (large to scale-like)

Stamens	Filaments	Anthers	Gynoecium	Ovary	Style	Stigma	Pollen morphology	Reference[b]
5 or 8 or 10, fertile, equal to unequal	free to united	dorsifixed, longitudinal or lateral dehiscence	central to adnate	stipitate	filiform	not peltate	tricolporate, coarsely striate	7, 8, 13, 17
8 to 15, unequal	free	dorsifixed, longitudinal dehiscence	central to adnate	stipitate, pubescent	filiform	capitate or truncate	tricolporate, psilate, striate	2–4, 7, 8, 15, 17, 18
10, diadelphous	free to slightly fused basally	dorsifixed, longitudinal dehiscence	glabrous, adnate	stipitate	elongate	capitate	tricolporate, reticulate, striate-reticulate	3, 7, 8, 15, 17, 18
10, fertile	free	dorsifixed, longitudinal dehiscence	centrally attached	stipitate, short	–	–	tricolporate, striate	1, 3, 7, 8, 17, 18
3 to 8, fertile	free to united	dorsifixed, longitudinal dehiscence	adnate	stipitate	–	–	tricolporate, reticulate, some in tetrads	3, 7, 8, 13, 17
10(16 to 25), diadelphous when immature	free	dorsifixed, longitudinal dehiscence	adnate	stipitate, pubescent	filiform, sigmoid	capitate, puncti-form	tricolporate, coarsely striate, striate-reticulate	1, 3, 5, 7–9, 14, 16–18
4, fertile; 4 staminoid, unequal	united	dorsifixed	adnate	stipitate, dense pubes-cence	filiform	truncate	tricolporate, rugulate to striate-reticulate	3, 7, 8, 17, 18
3 to 9, fertile, equal, some staminoidia	free	dorsifixed, longitudinal dehiscence	adnate	stipitate	filiform	not peltate	tricolporate, punctate, rugulate-punctate, striate	3, 7, 8, 13, 17
3 to 5, fertile	free to united	dorsifixed, longitudinal dehiscence	adnate	sessile or stipitate	filiform	–	striate	8, 13, 17
3 or 4 to 9, fertile, equal-unequal, with to without staminoidia	free to united	dorsifixed, longitudinal dehiscence	adnate	stipitate	–	–	tricolporate, striate	7, 8, 13, 17

(*continued*)

TABLE 1. (*continued*)

Family/ Group[a]	Genus	Habit/Range	Flower	Hypanthium	Bracteoles	Sepals	Petals
	Paramacrolobium J. Léonard	tree/Africa	zygom., bisexual	present	large, free, some persistent, valvate, high on pedicel	4 to 6	5 (1 large, 2 small, 2 smaller)
Connaraceae	*Burttia* Baker f. & Excell	shrub-tree/ Africa	heterodistylous	–	filiform, caducous	(4)5, subequal, imbricate, elliptic to lanceolate, pubescent	(4)5, subequal, free, spatulate, glabrous
	Connarus L.	liana-shrub-tree/Africa, Asia, America	heterostylous, bisexual	–	–	5, imbricate-valvate, connate, ovate to obovate, glandular-punctate	5, imbricate, free, elliptic to obovate, glandular
	Vismianthus Mildbr.	shrub-tree/ Africa	heterodistylous	–	lanceolate, caducous	5, subequal, imbricate, connate, elliptic-oblong, glandular	5, free, subequal, elliptic to lanceolate, glandular-glabrous
	Eocaesalpinia herendeenii	–	zygom., bisexual	short	2, valvate, high on pedicel	2 partial	4, closed, oblong

Abbreviations: zygom. = zygomorphic; adnate = adnate to side of hypanthium.
[a] Group arrangement according to Cowan and Polhill (1981a,1981b).
[b] 1. Léonard (1957); 2. Dwyer (1958); 3. Fasbender (1959); 4. Knapp-van Meeuwen (1970); 5. Sowunmi (1973); 6. Dickison (1979); 7. Graham and Barker (1981); 8. Watson and Dallwitz (1983); 9. Ferguson (1987); 10. Breteler and Brouwer (1989); 11, 12. Lemmens (1989a, 1989b); 13. Banks and Klitgaard (2000); 14–16. Tucker (2000, 2001, 2002); 17. Herendeen et al. (2003); 18. Direct observation by the authors, described herein.

These characters are similar to Fabaceae and certain genera of Connaraceae (Table 1). While morphological characters of apocarpous pod-like fruits suggest a Fabaceae-Connaraceae relationship (Dickison, 1981; Lemmens et al., 2004), recent molecular studies suggest that Fabaceae are more closely related to Surianaceae and Quillajaceae (Wojciechowski, 2003; Bello et al., 2009). Characters of *E. herendeenii* that are similar to Fabaceae but not Connaraceae include 2-merous flowers and four stamens. The striate-reticulate pollen morphology of *E. herendeenii* also rules out Connaraceae.

Within Fabaceae, characters such as bracteoles subtending a zygomorphic flower with four stamens, and a stipitate gynoecium adnate to the side of a hypanthium are diagnostic of the subfamily Caesalpinioideae, tribes Cassieae and Detarieae s.l. (Cowan, 1981; Watson & Dallwitz, 1983; Tucker, 2003). Although most legume flowers have 21 floral organs, a reduction in the number of floral organs is common in Caesalpinioideae (Tucker, 2003). *Eocaesalpinia herendeenii* has large, well-developed bracteoles, which is a character that distinguishes Detarieae s.l. from other tribes

Stamens	Filaments	Anthers	Gynoecium	Ovary	Style	Stigma	Pollen morphology	Reference[b]
3 or 5, fertile, unequal, with staminoidia	united	dorsifixed, longitudinal dehiscence	adnate	stipitate	–	–	coarsely reticulate	8, 13, 17
10	shortly connate at base, filiform	dorsiversatile, ovoid	–	pubescent	filiform	(sub) capitate, more or less bilobed	reticulate	6, 10
10, episepalous	united at base	–	–	stipitate	glandular	more or less bilobed	reticulate	6, 11, 12, 17
10, fertile	shortly connate at base, filiform	–	–	stipitate, glandular	filiform	subcapitate or more or less bilobed	reticulate/rugulate	6, 10
4, diadelphous	free, ca. 4 × 0.25	Longitudinal dehiscence, 1.25–1.5 × 0.5	adnate	stipitate, 4 × 1 mm	filiform, strong, curved	missing	striato-reticulate, monad	18

in the Caesalpinioideae (Bruneau et al., 2000). Also, anthers of *E. herendeenii* possess lateral slits, and we presume longitudinal dehiscence, a character found in Detarieae s.l., while Cassieae anther dehiscence is via basal or apical pores (Cowan, 1981; Watson & Dallwitz, 1983). Such pores are not evident in *E. herendeenii*.

Floral characters of *E. herendeenii* are not found in any extant Detarieae s.l. genera. Overall, characters such as bracteoles placed high on the pedicel, four petals, four stamens, and a gynoecium adnate to the side of a hypanthium can be found in extant genera of *Afzelia* Sm., *Anthonotha* P. Beauv., *Cryptosepalum* Benth., *Didelotia* Baill., and *Gilbertiodendron* J. Léonard. Exceptions are that *Afzelia* has small nonvalvate bracteoles, *Cryptosepalum* has 1 to 3 petals, *Gilbertiodendron* five petals, and *Didelotia* has a centrally attached gynoecium (Table 1). The pollen of these genera are generally striate, such as *Crudia* Schreb. (Fig. 1H), while striate-reticulate pollen are found in *Brownea* Jacq., *Hymenostegia* Harms, *Isoberlinia* Craib & Stapf ex Holland, *Lysidice* Hance, and *Schotia* Jacq. (Fig. 1G, Table 1).

Fabaceae fossil flowers in the Middle Eocene Claiborne Group of southeastern North America are represented by *Protomimosoidea* Crepet & Taylor, *Eomimosoideae* Crepet & Dilcher (Mimoseae), and papilionoid of the Sophoreae (Crepet & Dilcher, 1977; Daghlian et al., 1980; Crepet & Taylor, 1986; Herendeen & Dilcher, 1990; Crepet & Herendeen, 1992). While there are no previous reports of Detarieae s.l. flowers from the Claiborne Group (Herendeen et al., 1992), there

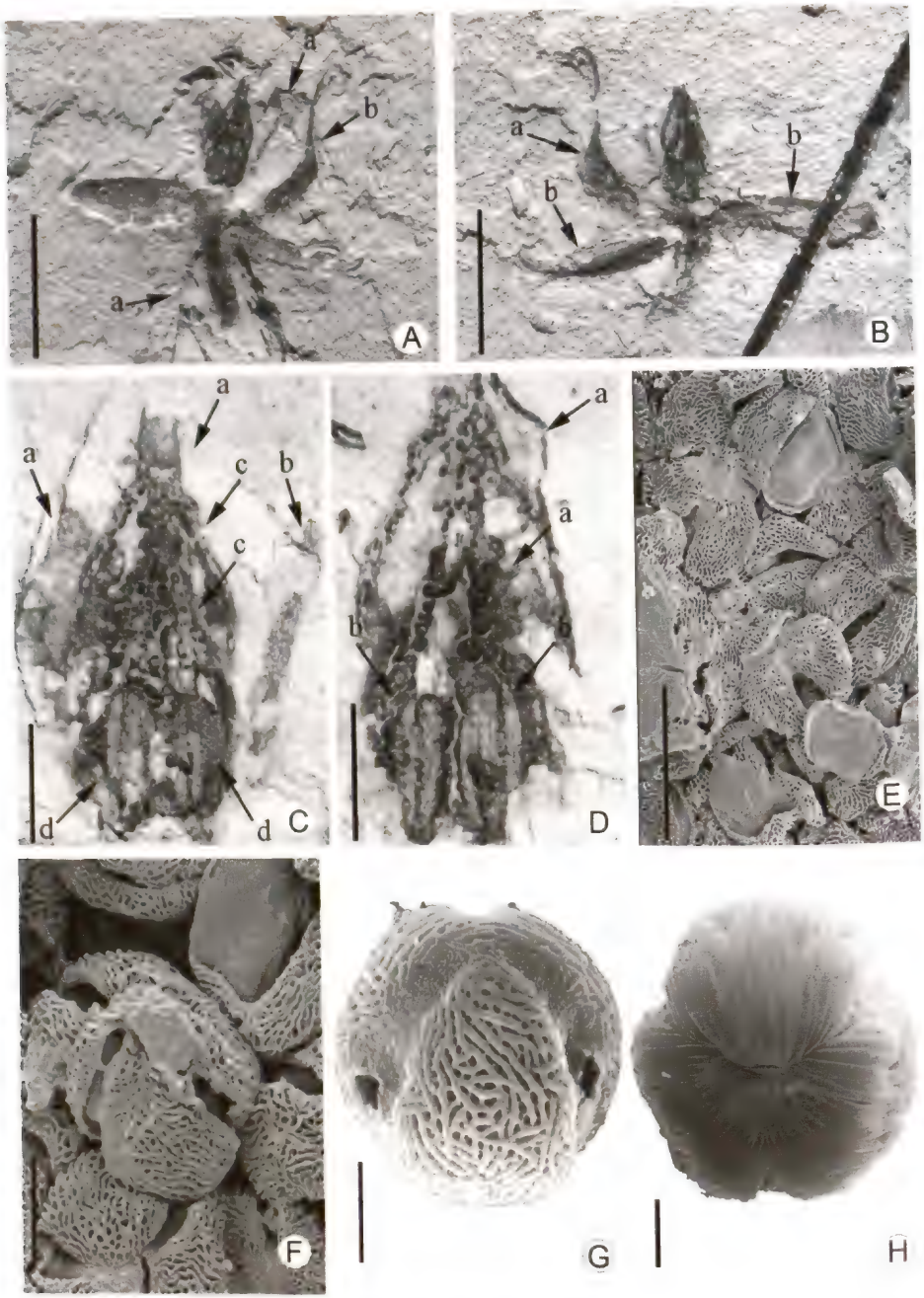

FIGURE 1. A–F. Flower and pollen of *Eocaesalpinia herendeenii* from the Middle Eocene of Tennessee (holotype UF 18903-30741). —A. Part. Filaments (arrows "a"); ovary (arrow "b"). —B. Counterpart. Ovary (arrow "a"); bracteoles (arrows "b"). —C. Part. Sepals (arrows "a"); filament (arrow "b"); petals (arrows "c"); anthers (arrows "d"). —D. Counterpart. Petals (arrows "a"); anthers (arrows "b"). —E. Pollen clump. —F. Pollen with torn colpi membrane. G, H. Extant pollen. —G. *Schotia latifolia* Jacq. —H. *Crudia reticulata* Mem. G, H courtesy of Alan Graham. Scale bars: A, B = 5 mm; C, D = 1 mm; E = 10 µm; F–H = 5 µm.

are fruits and leaflets of *Crudia* (Detarieae) from this group (Herendeen & Dilcher, 1990; Herendeen, 1992). One interesting similarity is the presence of petals in a semi-open position, found in flowers of *Podocarpium* (Benth.) Yen C. Yang & P. H. Huang in the Miocene of Europe (Liu et al., 2001). Although it is impossible to know the habit of *Eocaesalpinia herendeenii*, characters found in *E. herendeenii* are also found in seven extant genera of trees and shrubs of Africa (*Isoberlinia*, *Cryptosepalum*, *Didelotia*, *Schotia*, *Hymenostegia*, *Anthonotha*, and *Gilbertiodendron*), one from Africa/Asia (*Afzelia*), one in Asia (*Lysidice*), one from South America and the West Indies (*Brownea*), and one found throughout the tropics (*Crudia*) (Table 1).

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THE VASA PARK FLORA, KING COUNTY, WASHINGTON, U.S.A.: A WINDOW INTO THE LATE MIOCENE OF THE PACIFIC NORTHWEST

Richard M. Dillhoff, Thomas A. Dillhoff,* Anthony P. Jijina, and Caroline A. E. Strömberg**

ABSTRACT

A Late Miocene flora (11.4 ± 0.61 Ma) from Bellevue, Washington, is described using macro- and microfossils to summarize the flora and estimate climate and vegetation coverage. Genera recognized from macrofossils include pteridophytes (*Equisetum* L., *Woodwardia* Sm., and *Allantodiopsis* Knowlt. & Maxon, an apparent relict from the Eocene Puget Group flora), a rare cupressaceous conifer, and common angiosperms (*Platanus* L., *Cercidiphyllum* Siebold & Zucc., *Ulmus* L., *Fagus* L., *Hydrangea* L., *Alnus* Mill., *Acer* L., and *Persea* Mill.). Including unidentified morphotypes, the macroflora records one bryophyte, six pteridophytes, one gymnosperm, and 24 angiosperms. Well-preserved fossil pollen from the same sediments reveals a much richer regional flora. Although cupressaceous pollen is the most common element, a diverse record of Pinaceae is revealed by the palynoflora, including *Abies* Mill., *Picea* A. Dietr., *Pinus* L., *Pseudotsuga* Carrière/ *Larix* Mill., and *Tsuga* Carrière. In contrast, the Pinaceae are totally absent from the macrofossil record. Additional angiosperm genera identified from pollen include *Liquidambar* L., *Ilex* L., cf. *Sarcobatus* Nees, *Carya* Nutt., *Juglans* L., *Nyssa* L., *Fraxinus* L., and *Salix* L. Significant rare elements in the pollen flora include representatives of the Poaceae and Asteraceae. In total the palynomorph assemblage documents more than twice the diversity found in the macroflora. Coexistence analysis based on the pollen assemblage estimates mean annual temperature (MAT) of 11.6°C–16.6°C. Together, the macroflora and palynofloras suggest that Pacific Northwest plant communities—and climates—had not changed substantially since the Middle Miocene. Phytoliths recovered from the sediments suggest a closed-canopy forest with warm-adapted grasses of the PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae) clade in the understory or in forest gaps. Geological and botanical evidence indicate that the fossils are preserved in flood overbank deposits associated with widespread Late Miocene conglomerates found throughout western Washington.

Key words: geology, Miocene, paleobotany, palynology, phytoliths.

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We are pleased to participate in the Festschrift honoring Alan Graham on his 80th birthday. Alan's early fieldwork included the Middle Miocene sites at Trout and Sucker creeks in eastern Oregon. Alan used both macrofossils and palynomorphs to describe the local and regional flora of southeastern Oregon in the Middle Miocene. We will follow in his footsteps, using macrofossils, the palynoflora, and phytoliths, in addition to sedimentology, to describe the flora, paleoclimate, and paleoenvironment of the Vasa Park locality in the Late Miocene and compare Vasa with other Northwest Miocene occurrences (Fig. 1).

The site is located in a narrow ravine on land owned by a private park on the southern shore of Lake Sammamish in Bellevue, Washington. The majority of sedimentary exposures in the immediate vicinity of Vasa Park are the nearshore marine Oligocene sediments of the Blakely Formation and extensive Quaternary glacial deposits (Fig. 2). Tectonic activity along the Seattle fault created small isolated exposures of Miocene continental sediments, including the Vasa Park locality (Fig. 3). The Middle Miocene paleobotany of eastern Washington, eastern Oregon, and adjacent Idaho has been extensively documented by studies beginning over 100 years ago (Merriam, 1901; Knowlton, 1902, 1926; Chaney & Axelrod, 1959; Graham, 1963, 1965; Smiley, 1963; Smiley & Rember, 1985). These floras have documented floral evolution and vegetation change in the Pacific Northwest during this important time, characterized by substantial global warming associated with the Mid-Miocene Climatic Optimum (MMCO; Zachos et al., 2001). However, there is comparatively little data from the Late Miocene, especially in a coastal plain setting. As a result, our knowledge of the composition and structure of plant communities during the regional transition to a cooler and more seasonal climate has been extremely limited. Vasa Park provides an important new window into the Late Miocene environment of the Pacific Northwest.

Our data show that the Vasa Park flora is preserved in flood overbank deposits of a fluvial system. Large cobble conglomerates bracketing the fossil-bearing sediments record a high-energy environment, and the fossil-bearing sediments point

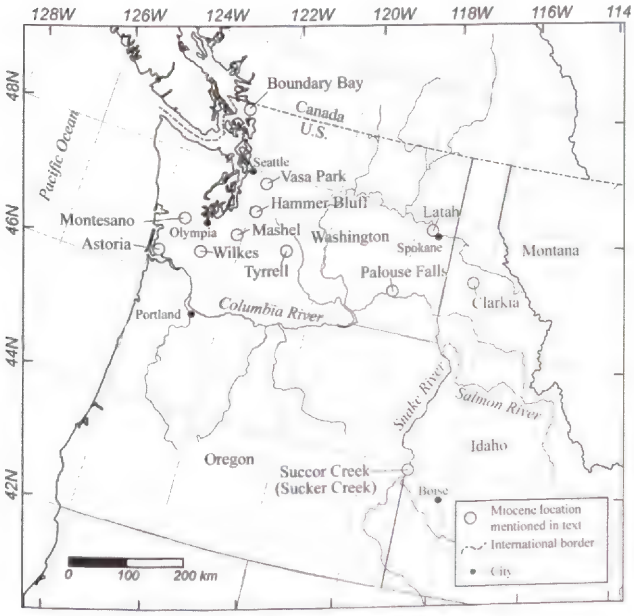


FIGURE 1. Pacific Northwest Miocene localities mentioned in the text.

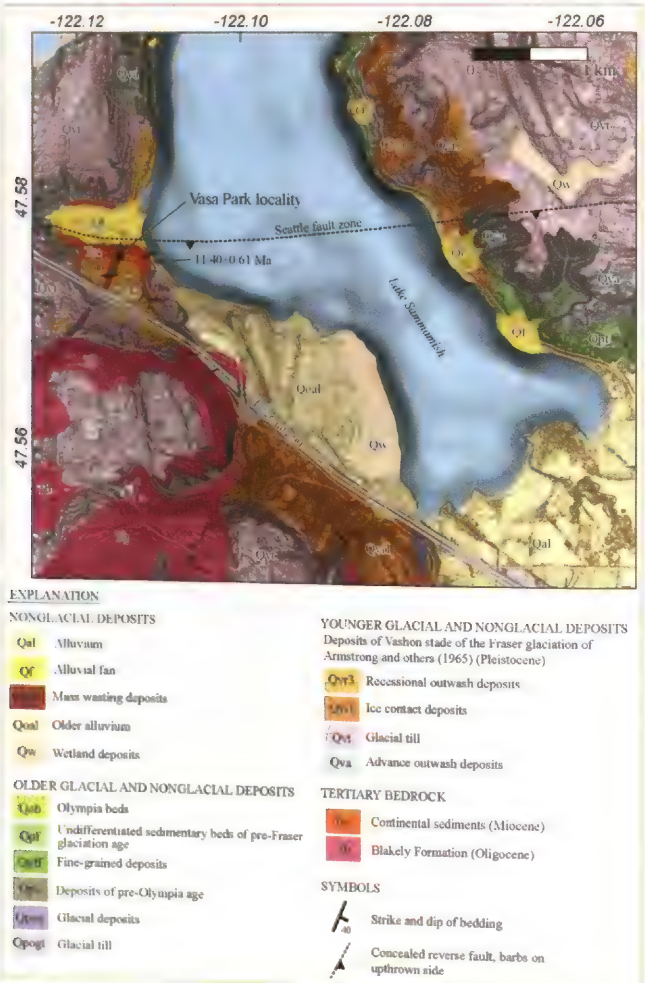


FIGURE 2. Geologic map of Vasa Park locality and surrounding area (Booth et al., 2012).

to a highly disturbed local environment subject to periodic inundation. The macroflora contains many species that grow in regularly disturbed fluvial environments and the most diverse assemblage of ferns known from a Northwest Miocene locality. The palynoflora records a diverse regional flora containing many elements that are not found in the macroflora. The climate estimate based on the palynoflora is of a warm temperate environment with ample precipitation during the growing season, similar to other Northwest Middle and Late Miocene deposits. Phytolith analysis shows the environment to have been primarily closed forest with only one horizon indicating a substantial presence of open habitat grasses.

GEOLOGIC SETTING

REGIONAL GEOLOGY

The Puget Lowland, a broad, low-lying region between the Cascade Mountains to the east and the Olympic Mountains to the west, is part of a

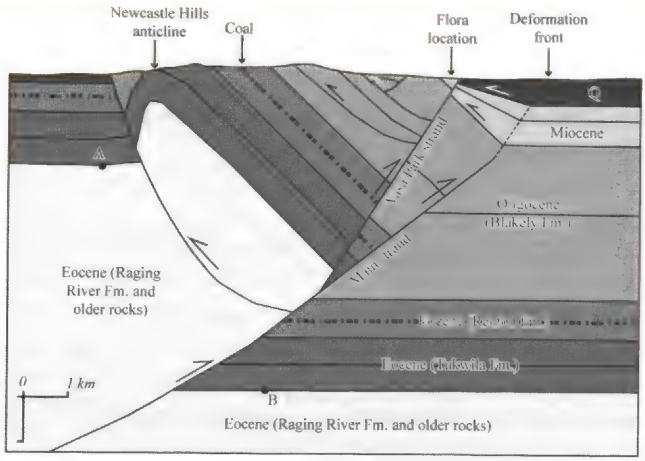


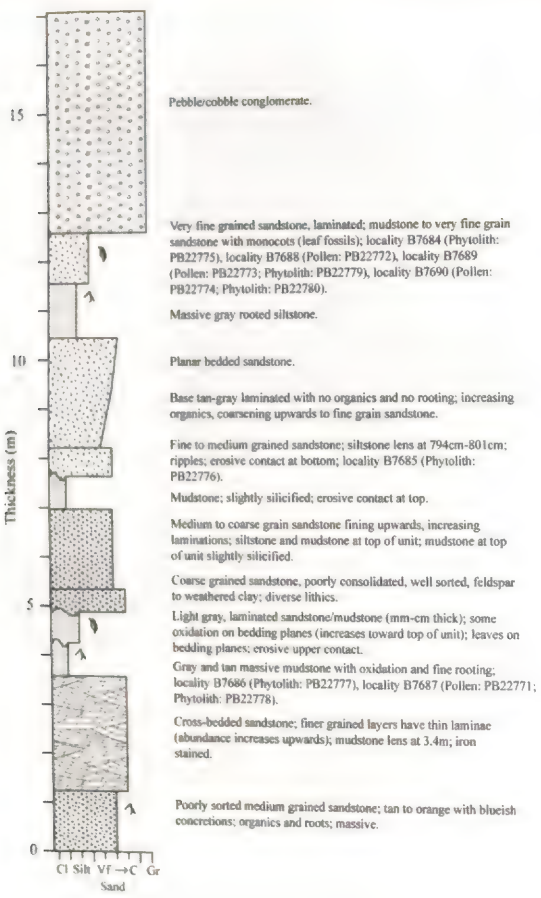
FIGURE 3. Stratigraphy of the Newport Hills anticline in the vicinity of Vasa Park. Redrawn from Liberty and Pratt (2008).

forearc basin formed in the Early Cenozoic that preserved Paleocene oceanic volcanic rocks and Eocene through Quaternary marine and terrestrial volcanic rocks and sedimentary deposits. Climate changes in the Quaternary resulted in a thick blanket of glacial deposits mantling bedrock. Eocene to Quaternary volcanic and sedimentary rocks lie beneath the glacial deposits in the central Puget Lowland, and north to south shortening warps these rocks into a series of east-west-trending folds (Wells et al., 1998; Brocher et al., 2001; Booth et al., 2004). The most prominent of these folds in the Seattle region are the Newcastle Hills and Gold Mountain anticlines; together these anticlines form a linear, northwest-trending bedrock extending almost 90 km across the central Puget Lowland (Mullineaux, 1970; Booth et al., 2012).

Outcrops of Miocene rocks at Vasa Park owe their exposure to profound tectonism along the north limb of the Newport Hills anticline, localized along a thrust fault—the Seattle fault— lying beneath the north limb of the anticline. Blakely et al. (2002), Johnson et al. (1994, 1999), and Liberty and Pratt (2008) identify several subparallel fault strands within an east-trending zone along the north side of the Newport Hills anticline using high-resolution aeromagnetic, geologic mapping, and seismic reflection methods. Rocks within the Newport Hills anticline consist of Eocene nonmarine arkosic sandstones with abundant plant fossils, Oligocene marine sandstones and siltstones with nearshore marine and plant fossil horizons, and minor amounts of conglomerate. These are overlain by Miocene nonmarine conglomerate, volcanic sandstone and siltstone, and mudstone, with local peat and tephra layers (Fig. 3). Booth et al. (2012) describe the Miocene deposits as outcrops of sandstone, conglomerate, tuff, and volcaniclastic sandstone above the southwest and southeast shores of Lake Sammamish. Interbeds of lignite contain nearly coherent logs. Bedding is concordant with underlying Oligocene marine deposits.

VASA PARK STRATIGRAPHIC SECTION

A 17-m-thick section at Vasa Park consists of three main units: a lower conglomeratic unit, a middle fine-grained unit, and an upper conglomeratic unit (the upper two parts are shown in a measured section on Fig. 4). Conglomerates are generally reddish brown (oxidized), matrix-supported pebble/cobble conglomerates with clast lithologies predominately of dark-colored, fine-


Thickness (m)
15
10
5
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Cl Silt Vf → C Gr
Sand
Pebble/cobble conglomerate.
Very fine grained sandstone, laminated; mudstone to very fine grain sandstone with monocots (leaf fossils); locality B7684 (Phytolith: PB22775), locality B7688 (Pollen: PB22772), locality B7689 (Pollen: PB22773; Phytolith: PB22779), locality B7690 (Pollen: PB22774; Phytolith: PB22780).
Massive gray rooted siltstone.
Planar bedded sandstone.
Base tan-gray laminated with no organics and no rooting; increasing organics, coarsening upwards to fine grain sandstone.
Fine to medium grained sandstone; siltstone lens at 794cm-801cm; ripples; erosive contact at bottom; locality B7685 (Phytolith: PB22776).
Mudstone; slightly silicified; erosive contact at top.
Medium to coarse grain sandstone fining upwards, increasing laminations; siltstone and mudstone at top of unit; mudstone at top of unit slightly silicified.
Coarse grained sandstone, poorly consolidated, well sorted, feldspar to weathered clay; diverse lithics.
Light gray, laminated sandstone/mudstone (mm-cm thick); some oxidation on bedding planes (increases toward top of unit); leaves on bedding planes; erosive upper contact.
Gray and tan massive mudstone with oxidation and fine rooting; locality B7686 (Phytolith: PB22777), locality B7687 (Pollen: PB22771; Phytolith: PB22778).
Cross-bedded sandstone; finer grained layers have thin laminae (abundance increases upwards); mudstone lens at 3.4m; iron stained.
Poorly sorted medium grained sandstone; tan to orange with blueish concretions; organics and roots; massive.

FIGURE 4. Stratigraphic section of Vasa Park sedimentary rocks. Burke Museum of Natural History and Culture, University of Washington (UWBM) locality numbers begin with "B"; UWBM sample numbers begin with "PB."

grained crystalline rocks and fine-grained andesitic and felsic volcanic rocks. The middle fine-grained part contains brownish gray tuffaceous siltstone, sandy siltstone, and silty sandstones. Volcanic fragments and tuffaceous material in finer-grained deposits commonly weather to clay. Lamination in finer-grained strata is common. A thick stratum of cross-bedded tuffaceous sandstone lies near the base of the section.

The stratigraphic position and low degree of lithification of the strata exposed in the creek section led some previous workers to assign a Quaternary age to these deposits (for example, Liesch et al., 1963). However, potassium-argon (K-Ar) ages from one nearby locality range from 9.3 to 14.7 Ma (Yount & Gower, 1991), and subsequent argon-argon (Ar/Ar) laser fusion dating from this same unit yielded an age of 11.40 ± 0.61 Ma (Booth et al., 2012).

Lithologies, sedimentary structures, and plant fossils suggest deposition in an alluvial system issuing from and between Miocene stratovolcanos located to the east. Conglomerates and interbedded sandstones are indicative of deposition in high-energy, nonglacial braided stream channels, and finer-grained sandstone and siltstone were deposited on the stream's floodplain. However, strata of fossiliferous silt, clay, and log-bearing lignite indicate that other parts of the deposit are fluviolacustrine in origin. The presence of poorly sorted,

thin, and interbedded fluvial and lacustrine sediments at Vasa Park suggests deposition in a low-relief piedmont environment characterized by floodplains and small lakes (possibly oxbow lakes).

CORRELATIVE UNITS

Exposures of Middle Miocene conglomerate and sandstone deposits throughout the Puget Lowland attest to widespread alluvial deposition in the Middle Miocene: the Hammer Bluff Formation near Enumclaw, Washington; the Mashel Formation near Orting, Washington; the Wilkes Formation near Toledo, Washington; and the Boundary Bay Formation (found in subsurface only) near Bellingham, Washington (Fig. 1). These deposits, like those at Vasa Park, suggest prevalent low-relief piedmont environments characterized by floodplains and small lakes in western Washington, with low hills to the east and west at the present locations of the Cascade and Olympic mountains (e.g., see Mullineaux, 1970). Leopold and Denton (1987) showed that the Columbia Plateau in eastern Washington did not take on its modern character until Pliocene or even Pleistocene time, suggesting that a significant moisture barrier at the present-day location of the Cascade Mountains did not exist in the Middle Miocene.

Middle to Late Miocene siltstones, sandstones, and conglomerates of the Astoria and Montesano formations outcrop west of Olympia, Washington, and fossils within each formation demonstrate deposition in shallow-water marine environments (Rau, 1967). The location of these marine deposits of similar age as nonmarine deposits found in the Puget Lowland suggest that the Middle to Late Miocene shoreline probably lay west of present-day Olympia.

MATERIALS AND METHODS

The Vasa Park locality occurs in a steep canyon that starts at the I-90 freeway and ends near the southwestern shore of Lake Sammamish in King County, Washington, located in T24N R5E. The exposure consists of approximately 17 m of mudstone, siltstones, and sandstone bracketed by massive beds of coarse, well-rounded basaltic conglomerate that has been documented across the Puget Sound region in association with the Seattle fault (see above; Blakely et al., 2002). Conglomerate layers often contain woody debris up to 50 cm in length, whereas leaves are preserved in fine-grained sandstones. Plant fossils (Figs. 5–7) typically occur along bedding planes separated by 1- to 5-cm sections of barren rock. The macroflora locality is designated as Burke Museum of Natural History and Culture, University of Washington locality UWBM 6816 (see Figs. 8 and 9 for microflora locality numbers within the section). Macrofossils were morphotyped using methods from the *Manual of Leaf Architecture* (Ellis et al., 2009).

Sediment samples (Figs. 8, 9) for pollen and phytolith analysis were collected from two main horizons. We did not attempt to collect incremental samples from the entire section, which consists largely of non-fossiliferous (based on preliminary sampling) sandstone; rather, in an attempt to provide an overview of the microfloral assemblages of the deposit, samples were collected from fine-grained exposures that are more likely to contain palynomorphs and phytoliths. Incremental stratigraphic sampling would be further complicated at this site because it is heavily vegetated, thus there is not a continuous exposure of the sediments. Two sediment samples (resulting in pollen or phytolith sample/specimen UWBM nos. PB22777 and PB22771/PB22778; see Fig. 9) were collected from a layer 0–75 cm below the leaf-bearing layer in gray and tan massive mudstone with oxidation and fine rooting sediment. Another four samples (resulting in pollen or phytolith sample/specimen UWBM nos. PB22772, PB22773/PB22779, and PB22774/PB22780; Figs. 8, 9) were collected from a single, fine-grained siltstone leaf-bearing exposure between 11.5 and 12 m from the base of the section.

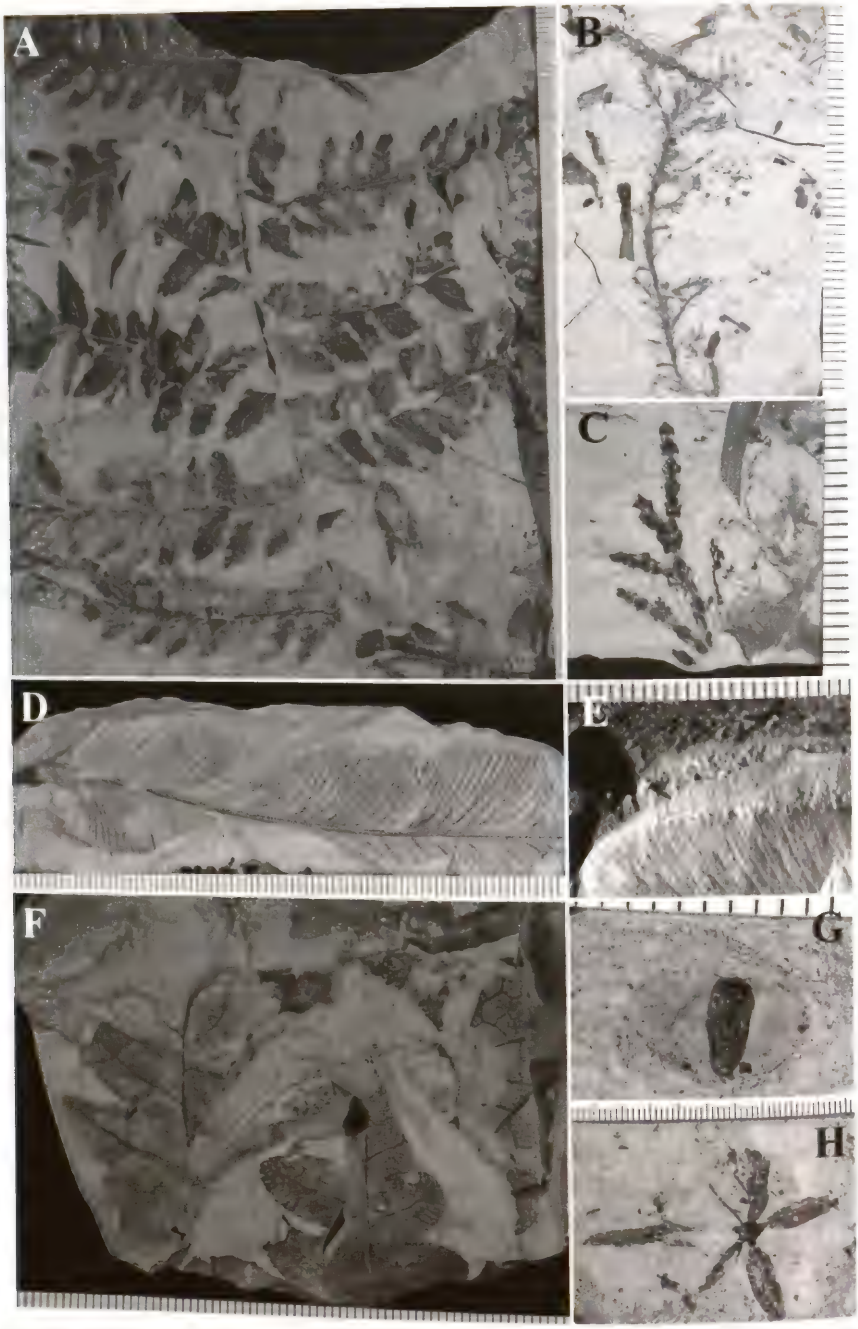

FIGURE 5. Pteridophytes and allies, bryophytes, and gymnosperms. —A. Dryopteridaceae (UWBM PB9440). —B. Gametophyte of unknown bryophyte (UWBM PB9474). —C. Foliage of *Chamaecyparis linguaefolia* (Lesquereux) MacGinitie (UWBM PB9698). —D. Pinnule of *Allantodiopsis* sp. (UWBM PB9613). —E. Serrate margin of *Allantodiopsis* sp. (UWBM PB9611). —F. Pinnules of *Woodwardia* sp. (UWBM PB9616). —G. Winged seed of *C. linguaefolia* (UWBM PB9766). —H. *Equisetum* sp. bulbils (UWBM PB9449).

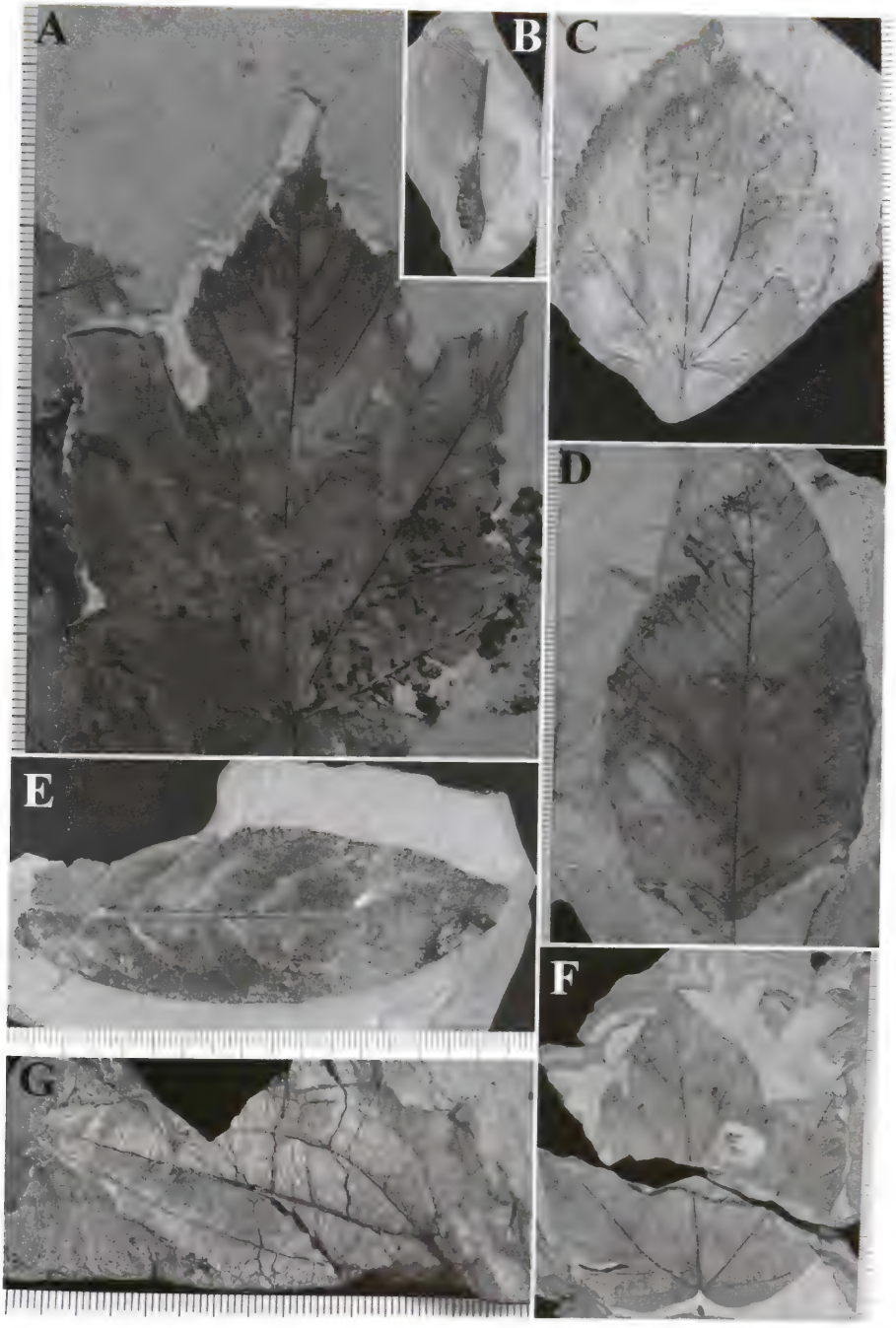

FIGURE 6. Vasa Park angiosperms. —A. Leaf of *Acer* sp. (UWBM PB89436). —B. Samara of *Acer* sp. (UWBM PB9961). —C. Leaf of *Cercidiphyllum crenatum* (Unger) Brown (UWBM PB9964). —D. Leaf of *Fagus washoensis* LaMotte (UWBM PB9538). —E. Leaf of *Persea pseudocarolinensis* Lesquereux (UWBM PB9960). —F. Leaf of cf. *Gossypium* sp. (UWBM PB9961). —G. Leaf of *Smilax magna* Chaney (UWBM PB9732).

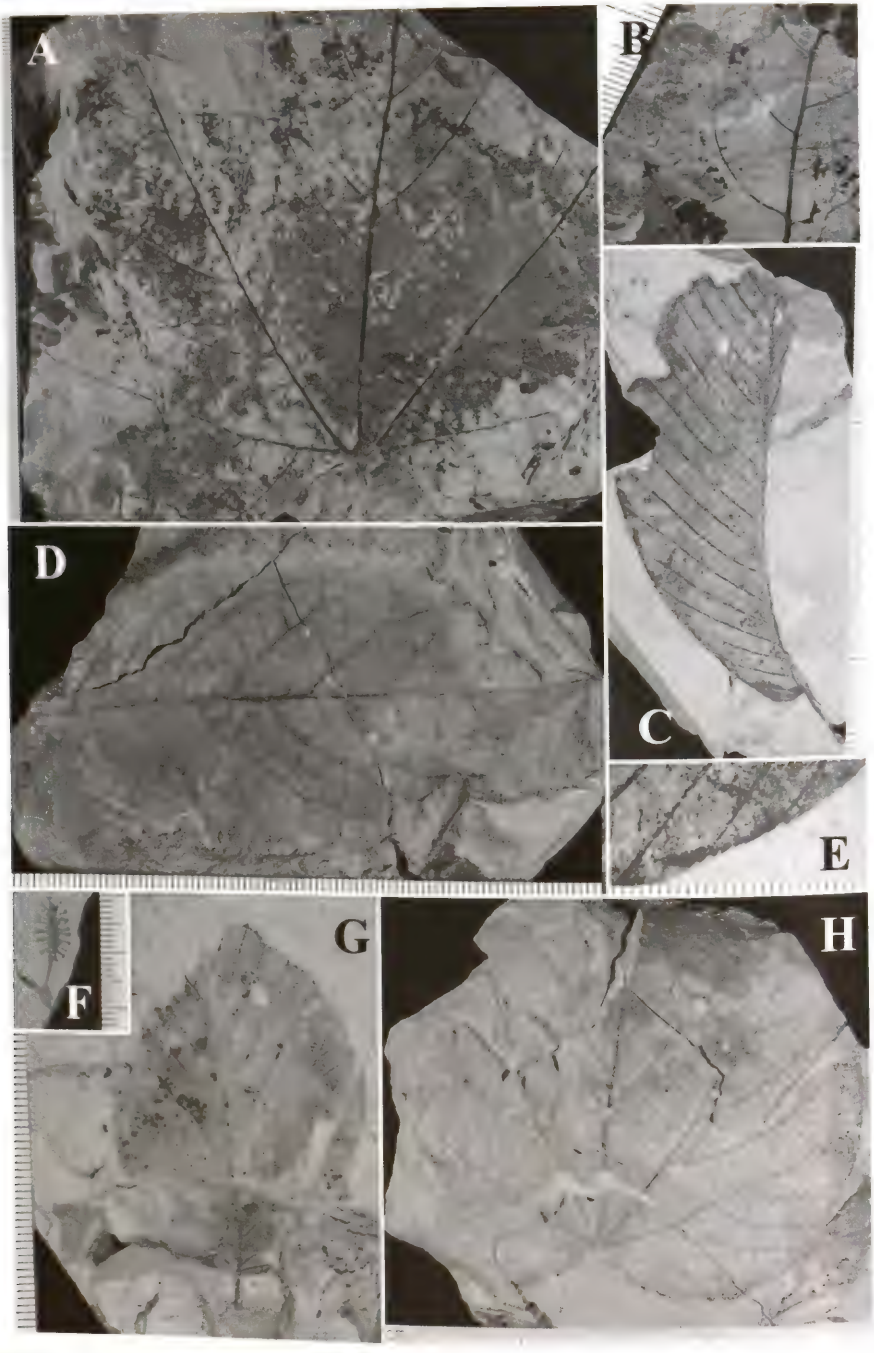

FIGURE 7. Vasa Park angiosperms continued. —A. Leaf of *Platanus dissecta* Lesquereux (UWBM PB9440). —B. Detail of A showing teeth. —C. Leaf of *Aesculus* sp. (UWBM PB9448). —D. *Hydrangea bendirei* (Ward) Knowlton (UWBM PB9944). —E. Detail of C showing teeth. —F. Infructescence of *Alnus* sp. (UWBM PB9605). — G. Leaf of *Alnus* sp. (UWBM PB9955). —H. Leaf of *Pauwlonia columbiana* Smiley (UWBM PB9588).

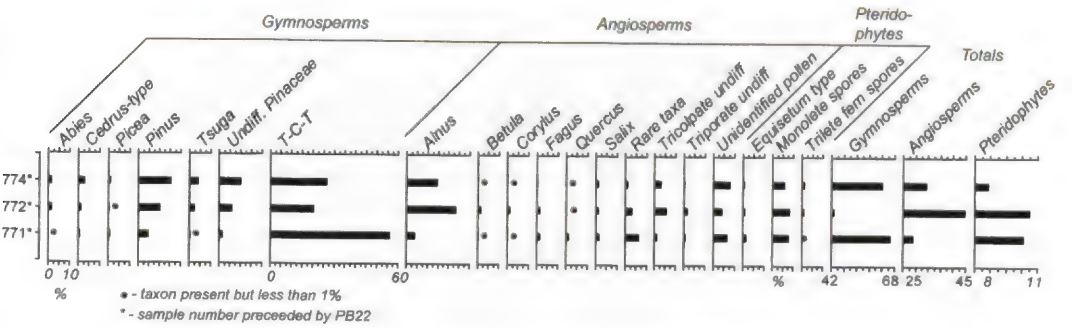

FIGURE 8. Vasa Park pollen diagram. TCT indicates pollen from the families Taxodiaceae, Cupressaceae, and Taxaceae.

Sample UWBM no. PB22774/PB22780 is closer to the modern creek bed, with approximately 2 m separating it from UWBM nos. PB22772 and PB22773/PB22779 (Fig. 8).

The sediment samples were processed for pollen using a modified version of the Faegri-Iversen method (Faegri & Iversen, 1964). Samples of the sediment matrix were washed and dried, then

		Phytolith morphotypes, relative abundance of total count (%)[1]														Tree cover[2]	
			FI TOT		GSSC	PACMAD TOT											
UWBM locality	Samples UWBM no.	AQ	Palm	Other FI	CH TOT	POOID-D	POOID-ND	PACMAD general	PAN	CHLOR	OTHG	NDG	NDO	Total phytolith count	FI	TOT+GSSC count	FI-t ratio (%)	FI-t ratio 95% C.I. (%)
B7687	PB22778	0.2	0.2	26.7	0	1.5	0.8	15.8	2	0	0.5	33	19.7	614	290		56.9	(51.6 - 62.8)
B7689	PB22779	2.9	0.1	23.1	0	0.2	0.1	0.8	0	0	0.3	38	34.2	1786	490		94.3	(91.9-96.2)
B7690	PB22780	0.7	0	52.9	0	0.5	0.2	2.2	0	0	0.2	22	21.7	548	311		94.5	(90.7-97.7)

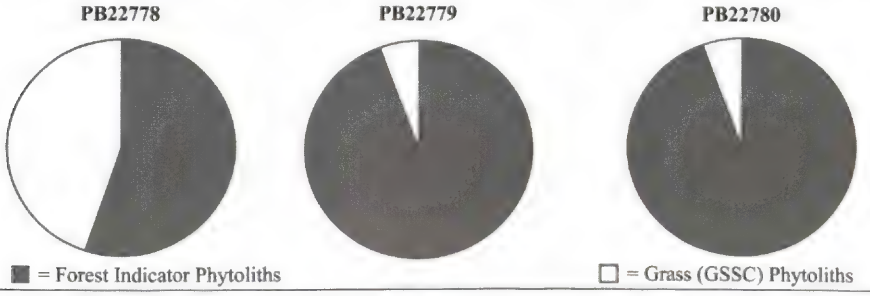

FIGURE 9. Relative abundance of phytolith morphotypes at Vasa Park. [1]AQ = phytoliths from wetland plants (e.g., *Equisetum*, sedges); Other FI = morphotypes typical of forest indicators (woody and herbaceous dicotyledons, ferns, conifers); GSSC = grass silica short cell; POOID-D = GSSC diagnostic of Pooideae; POOID-ND = GSSC produced in abundance by Pooideae but also present in other grasses; CH-TOT = GSSC of closed habitat grasses such as bamboos and basal grasses; PAN = GSSC typical of Panicoideae (many of which are C_4); CHLOR = phytoliths typical of Chloridoideae (C_4); PACMAD general = GSSC typical of PACMAD grasses (C_3/C_4); OTHG = nondiagnostic or unidentified GSSC; NDG = nondiagnostic (potential) grass phytoliths (e.g., cuneiform bulliforms, elongate sinuous, echinate, and dendritic, acicular hair base); NDO = nondiagnostic and unidentified non-GSSC phytoliths. [2]Tree cover is estimated using a rough proxy: FI-t = 100 × (Palm + Other FI)/(Palm + Other FI + GSSC). Confidence intervals are estimated using bootstrapping.

ca. 3 g of shale were crushed with a mortar and pestle and treated with 1 M hydrochloric acid (HCl) to remove carbonates. The samples were then rinsed with deionized water followed by an overnight soak in cold 48% hydrofluoric acid to remove silicates. The remaining material was rinsed twice in 1N HCl followed by two additional rinses with deinoized water to remove the acid residuals. After rinsing, the samples were washed through a 185-µm mesh Nitex filter to remove large particles, then through a 10-µm mesh Nitex filter to remove fine particles. The sample fraction remaining on the 10-µm mesh filter was treated by acetolysis to remove excess organics. Slides were prepared from the processed sample by mounting in glycerin jelly treated with 2% safranin dye. Of the four samples prepared for pollen analysis, one (UWBM PB22773) preserved only an insignificant amount of pollen and spores. The other three samples contained sufficient pollen and spores to allow detailed counting and analysis (Figs. 10–12).

Pollen slides were viewed at ×400 magnification under an optical light microscope to identify and photograph the different palynomorphs, and then counts of at least 500 grains were made for each sample to obtain relative abundances for the palynoflora. Pollen and spores were identified based on available literature (e.g., Wodehouse, 1935; Erdtman, 1952, 1957) and by comparison with modern pollen slides from the Jane Gray collection at the Burke Museum of Natural History and Culture, University of Washington.

Paleoclimate was estimated from the pollen assemblage using the coexistence approach developed by Mosbrugger and Utescher (1997). This method provides quantitative climate data based on the assumption that fossil taxa will have similar climatic requirements as their modern nearest living relative. After fossil pollen from the Vasa Park site was identified to the genus or family level as appropriate, quantitative climatic data for the modern representatives of these taxa were obtained from the Palaeoflora database (<http://www.palaeoflora.de>) and analyzed using the ClimStat program (Heinemann, 1998–1999). This program determines the zone where the climate requirements for the nearest living relatives of identified taxa overlap and provides a quantitative range for the analyzed parameters, including mean annual temperature, cold month mean temperature, warm month mean temperature, mean annual precipitation, wet month precipitation, dry month precipitation, and warm month precipitation.

In addition to the samples collected for both pollen and phytolith extraction, three sediment samples from other fine-grained paleosols (entisol; Soil Survey Staff, 2006) levels, as marked by root traces, were also collected, because fossil soils have been shown to contain the highest concentrations of phytoliths (Strömberg, 2004). Phytolith extraction was carried out following methods modified from Strömberg (2003, 2005). Approximately 1.2 g of sediment was treated with concentrated (12 M) HCl to remove carbonates, sieved through a 250-µm sieve to remove coarse particles, and treated with heated Schultze's solution to remove organic compounds. Clay particles were removed after deflocculation by sieving through a 53-µm sieve and repeated centrifuging. Finally, biogenic silica was isolated using heavy liquid ($ZnBr+HCl+H_2O$). From the extracted silica, multiple fixed microscope slides were prepared for counting and analysis using an optical light microscope under ×1000 magnification with immersion oil.

In samples considered sufficiently productive (UWBM nos. PB22778, PB22779, PB22780), at least 250 (290–490) diagnostic phytoliths (see definition below) were classified along with non-diagnostic phytoliths, to provide statistically robust counts for vegetation analysis (Strömberg, 2009), resulting in total counts of 548 to 1786 (Fig. 5). Rare phytolith morphotypes were noted to establish the presence of certain taxa, but not factored into the counts. Other biogenic silica, including diatoms, sponge spicules, and chrysophyte cysts, were noted for presence but not quantified.

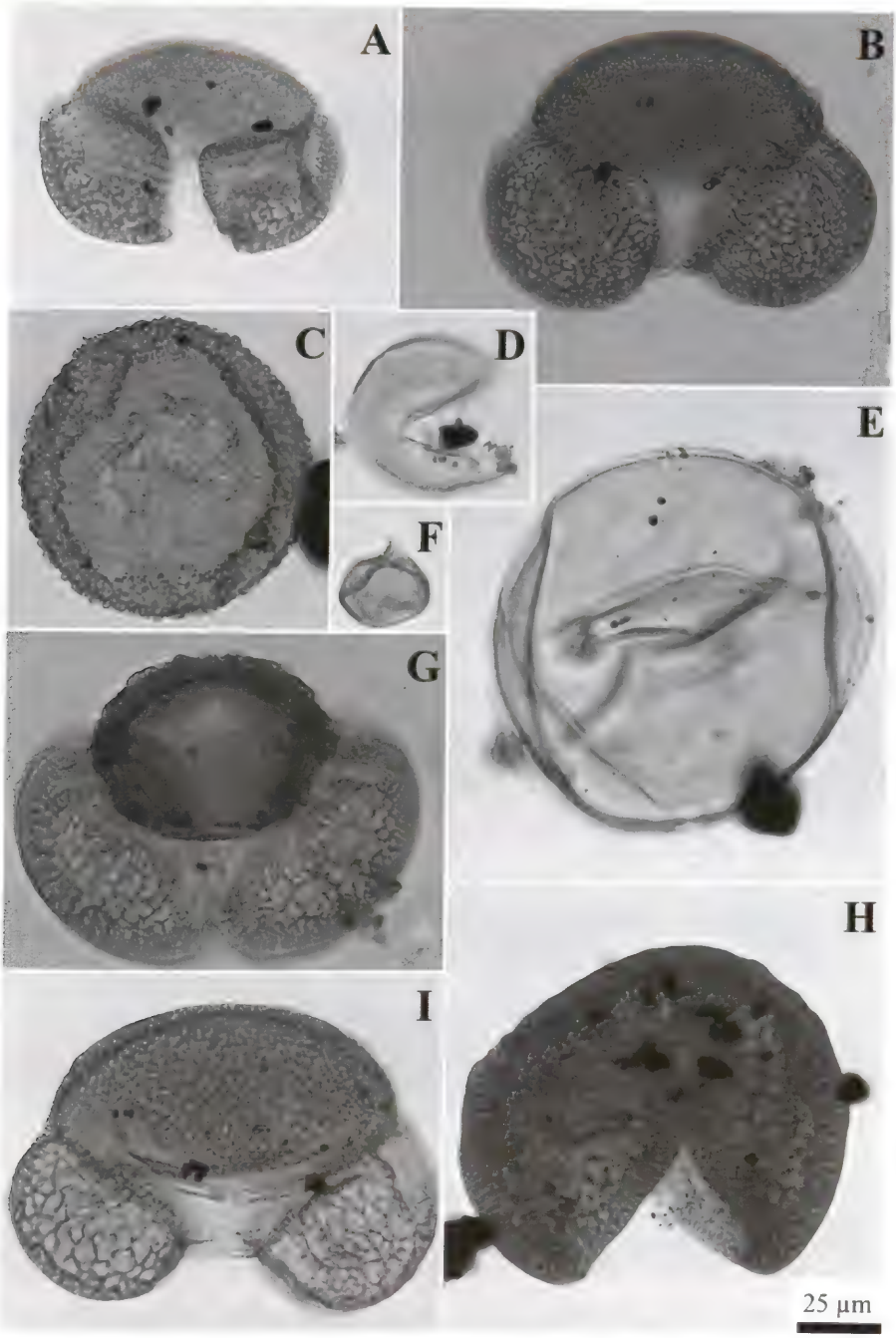

FIGURE 10. Vasa Park gymnosperm pollen. —A. *Picea* (slide no. UWBM PB22771A). —B. *Pinus* (UWBM PB22771C). —C. *Tsuga* (UWBM PB22771C). —D.TCT (UWBM PB22771A). —E. *Pseudotsuga/Larix* (UWBM PB22772A). —F. *Metasequoia/Sequoia* type (UWBM PB22771B). —G. Podocarpaceae/*Cathaya* type (UWBM PB22772D). —H. *Cedrus* (UWBM PB22771A). —I. *Abies* (UWBM PB22771C).

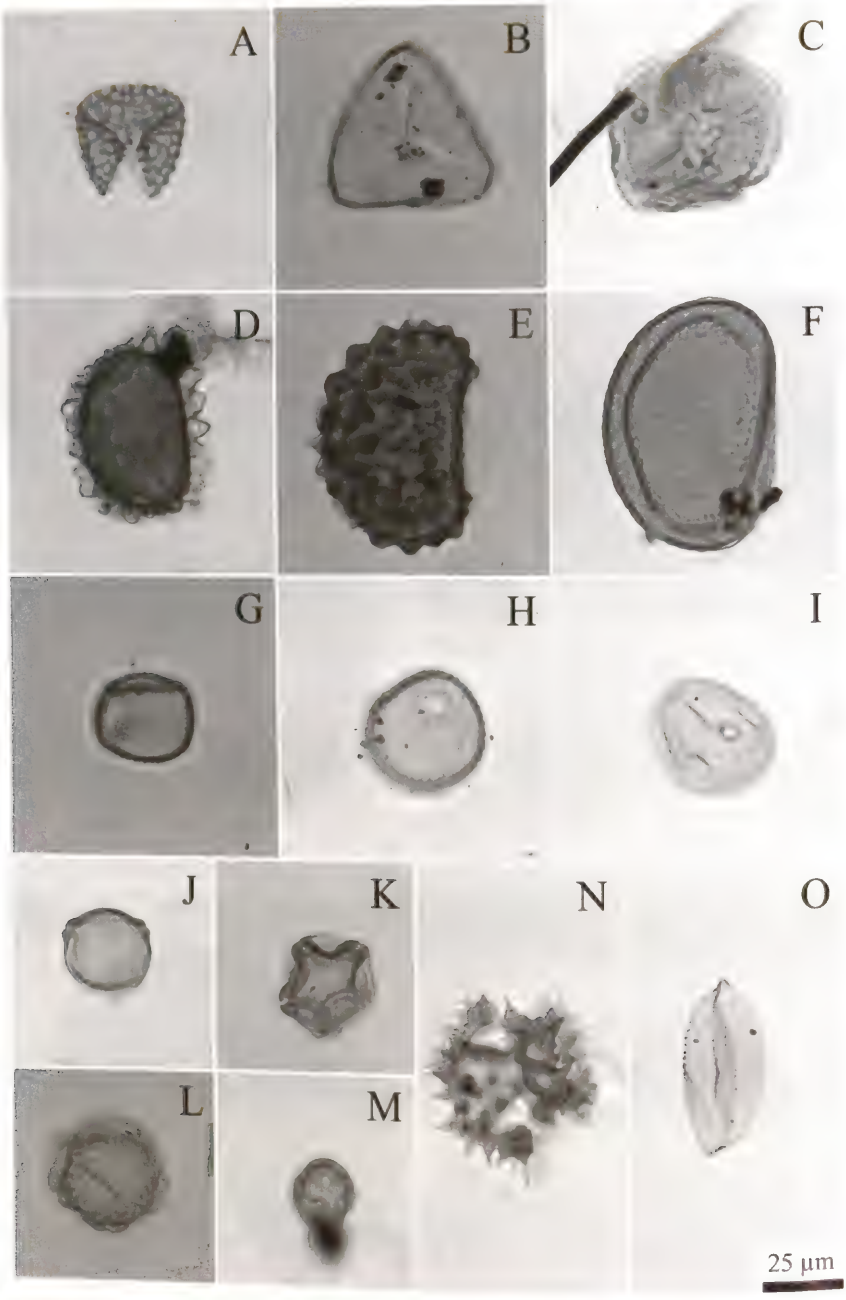

FIGURE 11. Vasa Park pteridophyte spores and angiosperm pollen. —A. *Lycopodium* (slide no. UWBM PB22771A). —B. Unidentified trilete spore (UWBM PB22774A). —C. *Selaginella* (UWBM PB22771D). —D. Dryopteridaceae (UWBM PB22771B). —E. Monolete spore (UWBM PB22771A). —F. Polypodiaceae (UWBM PB22771C). —G. *Potamogeton* (UWBM PB22772B). —H. Typhaceae (UWBM PB22772A). —I. Poaceae (UWBM PB22772A). —J. *Betula* (UWBM PB22771A). —K. *Alnus* (UWBM PB22771A). —L. *Ulmus* (UWBM PB22772B). —M. Cf. Chenopodiaceae (UWBM PB22771C). —N. Asteraceae (UWBM PB22772A). —O. Liliaceae (UWBM PB22771C).

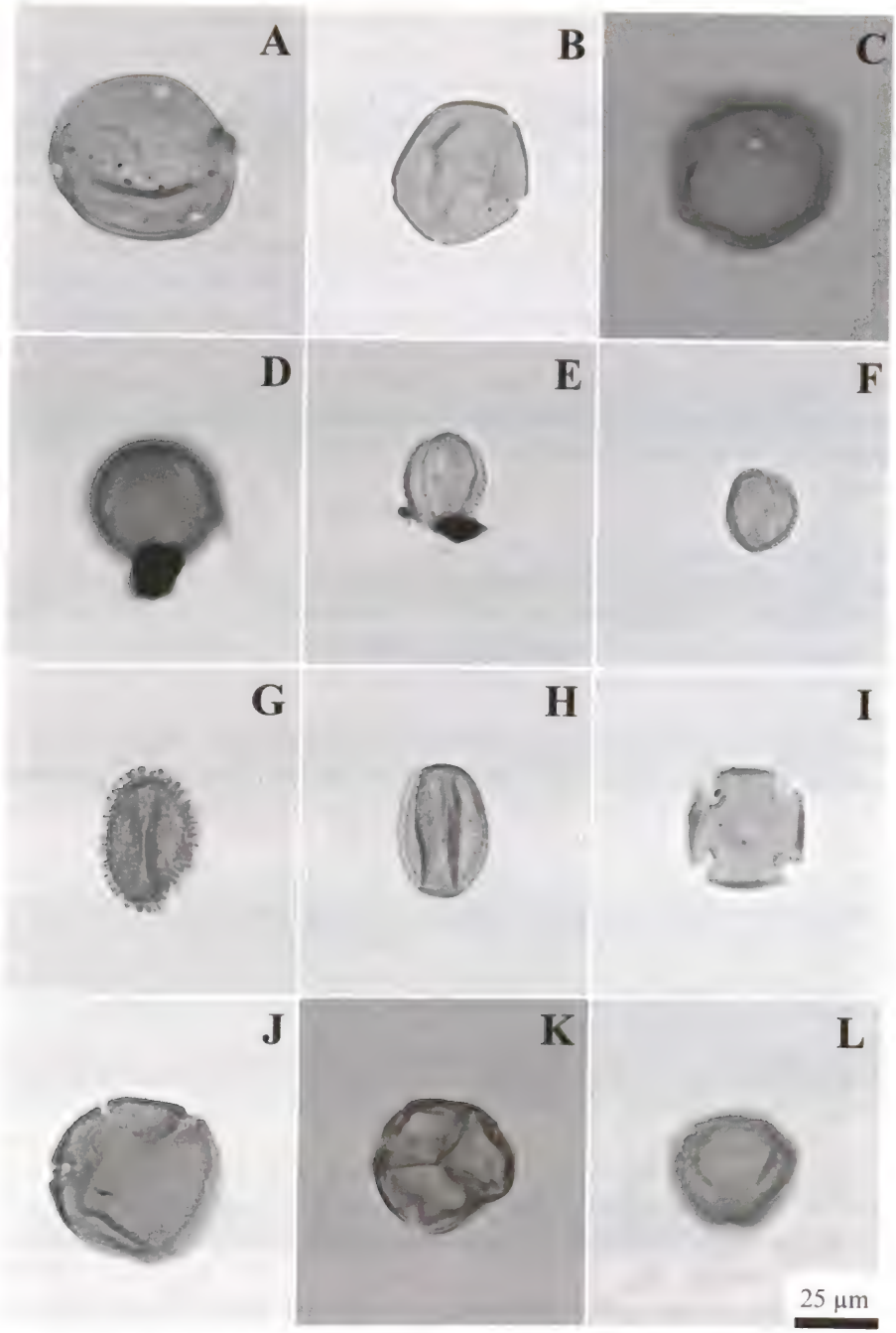

FIGURE 12. Vasa Park angiosperm pollen continued. —A. *Carya* (slide no. UWBM PB22772A). —B. *Pterocarya* (UWBM PB22771D). —C. *Juglans* (UWBM PB22772B). —D. *Liquidambar* (UWBM PB22771A). —E. *Salix* (UWBM PB22772A). —F. *Acer* (UWBM PB22771A). —G. *Ilex* (UWBM PB22771C). —H. *Quercus* (UWBM PB22771C). —I. *Fraxinus* (UWBM PB22772A). —J. *Fagus* (UWBM PB22771A). —K. Ericaceae (UWBM PB22772D). —L. *Nyssa* (UWBM PB22771D).

The fossil phytoliths were classified according to a scheme outlined in Strömberg (2004, 2005) and Strömberg et al. (2007a, 2007b) based on the literature (e.g., Piperno, 1988, 2006) and on description and analysis of a modern reference collection (Strömberg, 2003, unpublished data). Morphotypes were grouped into the following major categories: (1) forest indicator phytoliths (FI TOT), forming primarily in palms, woody or herbaceous dicotyledons, conifers, and ferns (Fig. 13G–J, L); (2) grass silica short cells (GSSC), found only in grasses, including forms indicative of closed-habitat grasses, such as bambusoid and basal grasses, and open-habitat grasses, such as pooid and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micraioideae, Aristidoideae, and Danthonioideae) grasses (Duvall et al., 2007; Aliscioni et al., 2012) (Fig. 13A–F); (3) phytoliths indicative of taxa typically growing in wetlands (AQ), including *Equisetum* L. and sedges (Fig. 13K); and (4) various nondiagnostic and unclassified forms.

Diagnostic phytoliths (FI TOT and GSSC) were used for reconstruction of vegetation type (e.g., forest, grassland) following Strömberg (2005) and Strömberg et al. (2007a, 2007b, 2013); specifically, types and abundances of forest indicator forms relative to grass silica short cells, as well as the composition of the GSSC assemblages, were examined. The so-called FI-t ratio (FI TOT/(FI TOT + GSSC)%) provided a rough estimate of tree cover; bootstrap 95% confidence intervals (unconditional case, using the total count as the sample size) for this metric was estimated using the software Resampling Stats (Simon, 1997). FI-t does not directly translate to percent tree cover, but a comparison of FI-t through time or space can allow inference of trends in openness through time (Strömberg, 2004, 2005, 2009).

Grass community composition was inferred by analyzing relative abundances of different grass types within the GSSC assemblages. Using bootstrapping methods (Resampling Stats), the fossil samples were statistically compared to grasses in a modern reference collection to account for overlap in morphotype production among major grass groups (see Strömberg, 2005, for detailed methods). Specifically, because the samples contained high relative abundance of PACMAD grasses they were tested to determine if pooid grasses may also have contributed to the GSSC assemblages (Strömberg 2005, 2009). In addition, the presence of particularly diagnostic morphotypes (certain crenate GSSC) was documented. Proximity to water is indicated by relative frequency of sedge phytoliths, as well as semiquantitative estimates of relative abundance of diatoms, chrysophyte cysts, and sponge spicules (Strömberg, 2005).

RESULTS

FLORISTIC STUDY

Taxa identified from macrofossil (Figs. 5–7) and palynomorph remains (Figs. 10–12) are summarized in Table 1.

Pteridophytes and allies (Figs. 5, 11).

Bryophyta. The vegetative gametophyte of an unknown bryophyte (Fig. 5B) is preserved at Vasa Park.

Lycopodiaceae. *Lycopodium* L. spores (Fig. 11A) are uncommon but present in all samples.

Selaginellaceae. *Selaginella* P. Beauv. spores with intact endospore (Fig. 11C) occur rarely in the pollen and spore assemblage.

Equisetaceae. *Equisetum* L. sp. (Fig. 5H). Compressions of small woody underground bulbils arranged radially in groups of five are relatively common at Vasa Park. A few specimens representing nodal sheaths from fertile shoots have also been recognized (not figured). This represents the first confirmed occurrence of *Equisetum* macrofossils in the Miocene of Washington. The specimen figured as an underground stem of *Equisetum* from the Middle Miocene Latah Formation by Knowlton (1926: plate IX, fig. 1) is a stem with attached *Nordenskioldia* Heer fruits. An *Equisetum* rhizome and stem were found at the

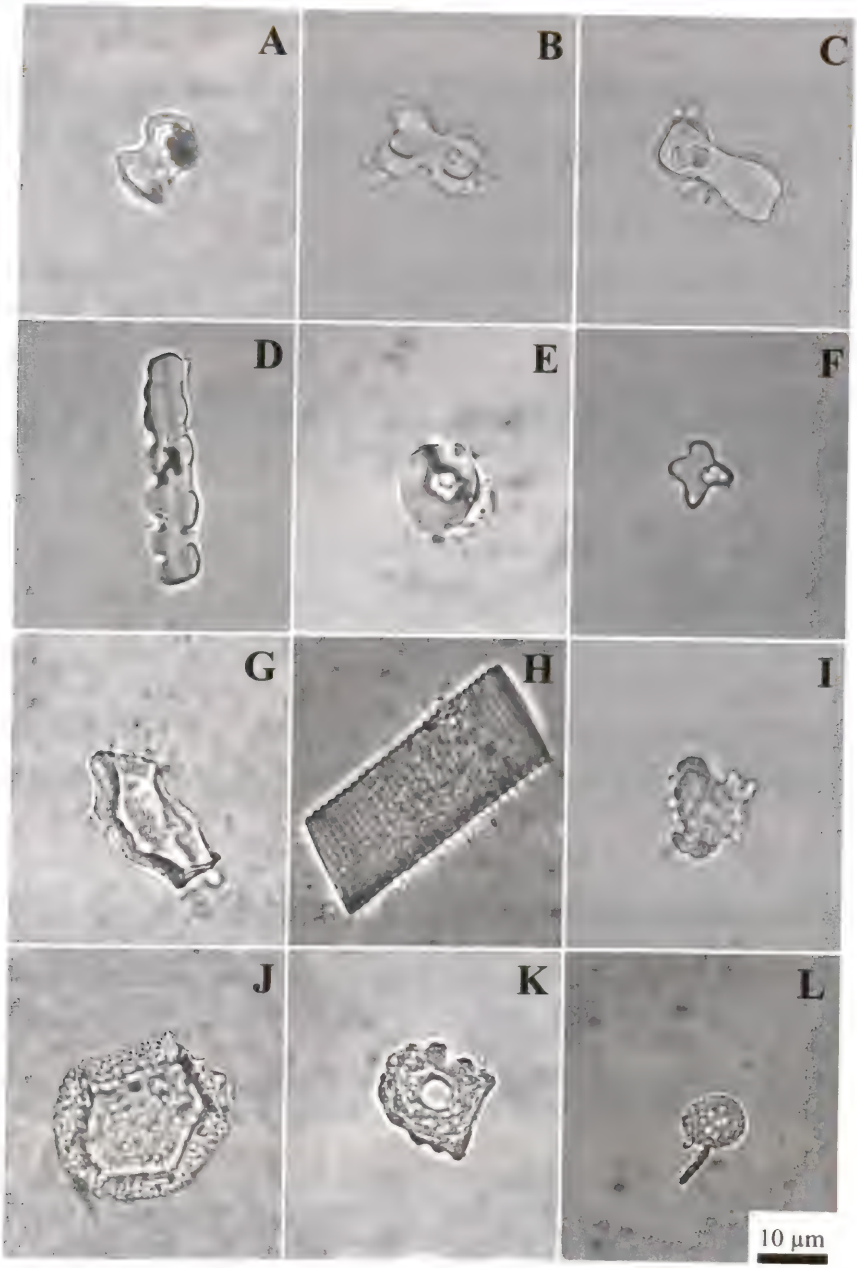

FIGURE 13. Phytoliths from Vasa Park. A–F. Grass silica short cells (Poaceae). A–C. Bilobates (PACMAD grasses). —A. Simple lobate (UWBM PB22778G). —B. Inverted bilobate (UWBM PB22778M). —C. Almost panicoid bilobate (UWBM PB22778B). —D. Crenate (Pooideae) (UWBM PB22779C). —E. Keeled rondel (Pooideae?) (UWBM PB22778I). —F. Cross (Panicoideae/PACMAD) (UWBM PB22778B). G–J. Forest indicator phytoliths. —G. Sclereid element (typical of woody dicotyledons) (UWBM PB22778C). —H. Tracheary element (dicotyledons and other forest indicator taxa) (UWBM PB22779B). —I. Large nodular body (woody dicotyledons) (UWBM PB22778B). —J. Polyhedral epidermis (dicotyledons) (UWBM PB22778E). —K. Epidermal sedge plate (Cyperaceae) (UWBM PB22780E). —L. Echinate (spiky) sphere (Palmae?) (UWBM PB22779D).

TABLE 1. Vasa Park combined flora from macrofossils and palynomorphs.

Group/Family	Taxon	Macrofossils	Pollen/Spores	Figure
Bryophytes	undetermined genus	G		Fig. 5B
Lycophytes				
Lycopodiaceae	*Lycopodium* sp.		Sp	Fig. 11A
Selaginellaceae	*Selaginella* sp.		Sp	Fig. 11C
Pteridophytes				
Equisetaceae	*Equisetum* sp.	B, Ns	Sp?	B = Fig. 5H; Ns not figured
Blechnaceae	*Woodwardia* sp.	L		Fig. 5F
Dryopteridaceae	*Allantodiopsis* sp.	L		Fig. 5D, E
	undetermined genus	L	Sp	Fig. 5A; Fig. 11D
Polypodiaceae	undetermined genus		Sp	Fig 11F
Monolete spores	undetermined genus		Sp	Fig. 11E
Trilete spores	undetermined genus		Sp	Fig. 11B
Gymnosperms				
Cupressaceae	*Chamaecyparis linguaefolia* (Lesquereux) MacGinitie	Lt, S		Fig. 5C, G
	Sequoia/*Metasequoia* sp.		P	Fig. 10F
TCT	undetermined genus		P	Fig. 10D
Pinaceae	*Abies* sp.		P	Fig. 10I
	Cedrus sp.		P	Fig. 10H
	Picea sp.		P	Fig. 10A
	Pinus sp.		P	Fig. 10B
	Pseudotsuga/*Larix* sp.		P	Fig. 10E
	Tsuga sp.		P	Fig. 10C
Incertae sedis	*Podocarpidites*/*Cathaya* sp.		P	Fig. 10G
Angiosperms				
Monocotyledons				
Liliaceae	undetermined genus		P	Fig. 11O
Poaceae	undetermined genus		P	Fig. 11I
Potamogetonaceae	*Potamogeton* sp.		P	Fig. 11G
Smilacaceae	*Smilax magna* Chaney	L		Fig. 6G
Typhaceae	*Typha*/*Sparganium* sp. (monad)		P	Fig. 11H
Dicotyledons				
Altingiaceae	*Liquidambar* sp.		P	Fig. 12D
Aquifoliaceae	*Ilex* sp.		P	Fig. 12G
Asteraceae	undetermined genus		P	Fig. 11N
Betulaceae	*Alnus* sp.	I, L	P	Fig. 7G, F; Fig. 11K
	Betula sp.		P	Fig. 11J
	Carpinus/*Ostrya* sp.		P	not figured
	Corylus sp.		P	not figured
Cercidiphyllaceae	*Cercidiphyllum crenatum* (Unger) Brown	L		Fig. 6C
	cf. *Cercidiphyllum* sp.		P	not figured
Chenopodiaceae	undetermined genus		P	Fig. 11M
Ericaceae	undetermined genus		P	Fig. 12K

TABLE 1. (*continued*)

Group/Family	Taxon	Macrofossils	Pollen/Spores	Figure
Fagaceae	cf. *Castanea* sp.		P	not figured
	Fagus washoensis LaMotte	L		Fig. 6D
	Fagus sp.		P	Fig. 12J
	Quercus sp.		P	Fig. 12H
Juglandaceae	*Carya* sp.		P	Fig. 12A
	Pterocarya sp.		P	Fig. 12B
	Juglans sp.		P	Fig. 12C
Hydrangeaceae	*Hydrangea bendirei* (Ward) Knowlton	L		Fig. 7D
Lauraceae	*Persea pseudocarolinensis* Lesquereux	L		Fig. 6E
Magnoliaceae	undetermined genus		P	not figured
Malvaceae	cf. *Gossypium* sp.	L		Fig. 6F
Nyssaceae	*Nyssa* sp.		P	Fig. 12L
Oleaceae	*Fraxinus* sp.		P	Fig. 12I
Onagraceae	undetermined genus		P	not figured
Platanaceae	*Platanus dissecta* (Lesquereux)	L		Fig. 7A, B
	Platanus sp.		P	not figured
Salicaceae	*Salix* sp.		P	Fig. 12E
	cf. *Populus* sp.		P	not figured
Sapindaceae	*Acer* sp.	L, S	P	Fig. 6A, B; Fig. 12F
	Aesculus sp.	L		Fig. 7C, E
Ulmaceae	*Ulmus speciosa* Newberry	L		not figured
	Ulmus sp.		P	Fig. 11L

Abbreviations: B = bulbil; G = gametophyte; I = infructescence; L = leaves; Lt = leafy twigs; Ns = nodal sheath; S = seeds; P = pollen; Sp = spore; TCT = Taxodiaceae–Cupressaceae–Taxaceae pollen.

Sucker and Trout creeks Middle Miocene localities in southeastern Oregon (Graham, 1963, 1965). Stems and similarly preserved bulbils of *Equisetum* occur in the nearby Paleocene/Eocene Chuckanut Formation (Pabst, 1968). *Equisetum*-type spores (not figured) are common in all spore-pollen samples. There is some question as to whether these actually represent *Equisetum* or *Larix* Mill., since these two types are similar. The relatively small size of this palynomorph (32–40 µm), the inferred floodplain environment, and the presence of *Equisetum* macrofossils make it likely that this taxon is represented in the palynoflora.

Blechnaceae. *Woodwardia* Sm. sp. (Fig. 5F). Small pinnules of *Woodwardia* are a relatively common component of the pteridophyte flora at Vasa. The Vasa Park species most closely resembles modern *Woodwardia fimbriata* Sm., still found in western Washington (Pigg et al., 2006). *Woodwardia* has also been described from the Middle Miocene Sucker Creek, Idaho, and Yakima Canyon, Washington localities (Graham, 1965; Pigg & Rothwell, 2001).

Dryopteridaceae. *Allantodiopsis* Knowlt. & Maxon sp. (Fig. 5D, E). Pinnules with the characters of the extinct genus *Allantodiopsis* are not uncommon at Vasa. *Allantodiopsis* was widespread in the Paleocene and Eocene of the Rocky Mountain area (Brown, 1962; Wing, 1987) and also recognized from the Paleocene-Eocene Chuckanut and Puget Group formations of western

Washington (Pabst, 1968; Wolfe, 1968). Wolfe (1968) differentiated *A. pugetensis* Wolfe based primarily on unbranched secondary veins. The Vasa species typically has branched secondaries, or occasionally twice branched, as seen in *A. erosa* (Lesquereux) Pabst.

The phylogenetic position of *Allantodiopsis* among the ferns is uncertain (Collinson, 2001). The association of the single specimen of fertile material associated with the common sterile foliage that is the basis for the genus name has been questioned (McIver & Basinger, 1993). Similar foliage originally assigned to *Allantodiopsis* from the Eocene of Oregon was determined based on the cuticle to be an extinct cycad with fernlike foliage, *Eostangeria barthel* (Kvaček & Manchester, 1999). In that genus secondaries sometimes reunite at the margin, forming loops, but secondaries in the Vasa specimens do not. The Vasa Park occurrence dramatically extends the known stratigraphic occurrence of *Allantodiopsis*.

In addition to *Allantodiopsis*, foliage of a second member of the family, morphotype VP003 (Fig. 5A), is recognized as a member of the Dryopteridaceae. In the absence of fertile material it is not possible to assign this material to a genus; it could represent a bipinnate *Polystichum* Roth or *Dryopteris* Adans. The pinnule morphology of the fossil resembles modern *P. dudleyi* Maxon found in coastal California. Spores of the Dryopteridaceae type (Fig. 11D) are also present in the palynoflora.

Pteridophyte spores are diverse and constitute a significant percentage of all palynological samples. Monolete spores without preserved perine of the *Laevigatosporites* Ibrahim type (not figured) are common throughout the deposit. In addition, there are four distinct types with well-preserved perine; three of these are figured (Fig. 11D–F). Trilete spores are less common but still diverse, with at least two types without preserved perine (Fig. 11B), and three distinct types with preserved perine.

Gymnosperms (Figs. 5, 10).

Cupressaceae s.l. *Chamaecyparis linguaefolia* (Lesquereux) MacGinitie (Fig. 5C, G). *Chamaecyparis* Spach macrofossils have been identified from foliage, seeds, and a possible ovulate cone. The genus has also been identified from the Middle Miocene at Clarkia, Idaho (Smiley & Rember, 1985) and Trout Creek in southeastern Oregon (Graham, 1963). MacGinitie (1933) identified this taxon at Trout Creek and later identified it as *C. linguaefolia* (MacGinitie, 1953). The Vasa Park species is consistent with the Trout Creek occurrence. *Chamaecyparis* was also identified in coeval sediments from the nearby Late Miocene Hammer Bluff Formation (Mullineaux, 1970).

Metasequoia Hu & W. C. Cheng/*Sequoia* Endl. type (Fig. 10F). Rare cupressaceous pollen grains with papillae are found in all samples. The overall morphology is most similar to *Metasequoia*/*Sequoia*, but other cupressaceous genera are known to have papillae, including *Taxodium* Rich. and *Glyptostrobus* Endl. All four of these genera have been reported as macrofossils from the Miocene of the Pacific Northwest (Chaney & Axelrod, 1959; Graham, 1965; Smiley & Rember, 1985). In the absence of co-occurring macrofossils from Vasa Park, it is difficult to assign this pollen type to a particular genus.

The palynoflora also contains a large proportion of cupressaceous Taxodiaceae–Cupressaceae–Taxaceae (TCT) pollen (Fig. 10D).

Pinaceae. *Abies* Mill. (Fig. 10I). Two distinct types of *Abies* pollen have been noted in the palynoflora. *Abies* pollen is rare, but present in all pollen-bearing samples. The first type is quite large (155–187 μm) and is the one most often encountered. The figured type is smaller and is similar to modern *A. amabilis* Douglas ex J. Forbes, which is extant in the Pacific Northwest.

Cedrus Trew sp. (Fig. 10H). *Cedrus* pollen is a minor element in all samples from Vasa Park. This type is widespread in the Miocene of the Pacific Northwest, although to our knowledge

there have been no reports of confirmed *Cedrus* macrofossils.

Picea A. Dietr. (Fig. 10A). There are two types of *Picea* pollen found in the Vasa Park palynoflora: one is particularly large at up to 170 µm, while the other is smaller (90–97 µm). *Picea* is well represented throughout the Cenozoic of the Pacific Northwest and is widely reported in the Miocene.

Pinus L. sp. (Fig. 10B). *Pinus* is a common element of the Vasa Park palynoflora, contributing between 5% and 15% of the total pollen count.

Pseudotsuga Carrière/*Larix* Mill. type (Fig. 10E). Pollen of *Pseudotsuga* and *Larix* is very similar, thus they are reported as a single palynomorph. The large size of the grains (101–109 µm) indicates that they most likely represent *Pseudotsuga*. *Pseudotsuga* macrofossils are not common in the fossil record of the region, but foliage and cones have been reported from the Miocene of Oregon (Chaney & Axelrod, 1959; Graham, 1965). Recently, *Pseudotsuga* has been confirmed from the Middle Miocene of Washington based on well-preserved wood from the Ginkgo Petrified Forest (Wheeler & Dillhoff, 2009). To our knowledge, there have been no confirmed reports of *Larix* macrofossils from the Miocene of the Pacific Northwest.

Tsuga Carrière (Fig. 10C). *Tsuga* pollen is represented by two distinct types. One type is similar to modern *T. heterophylla* (Raf.) Sarg., which is extant in the Pacific Northwest. Similar pollen has been figured from the Clarkia deposit of Idaho (Gray, 1985). The second type is superficially similar to *T. canadensis* (L.) Carrière, but under high magnification it has visible spines, which are lacking in *T. canadensis*. This type may be more closely related to some of the modern Asiatic species of *Tsuga*, which are similar in morphology and have small spines.

Incertae sedis. There are two bisaccate pollen types (Fig. 10G) similar to those reported as *Podocarpus* Persoon or *Podocarpidites* Cookson ex Couper from other Cenozoic floras of the Pacific Northwest (Barnett & Fisk, 1980; Reininck-Smith & Leopold, 2005). Zetter et al. (2011) state that pollen of this type may also represent *Cathaya* Chun & Kuang, and that the pollen can only be reliably distinguished using features visible under SEM. Because of this uncertainty, these types are reported as Podocarpaceae/*Cathaya*. There have been no confirmed macrofossils of *Podocarpus* reported from the Cenozoic of the Pacific Northwest, while cones and foliage with preserved cuticle of *Cathaya* were described from the Middle Miocene Clarkia deposit of western Idaho (Kvaček & Rember, 2000).

Angiosperms, Monocotyledons.

Liliaceae. Several pollen grains attributed to the Liliaceae (Fig. 11O) were found at Vasa Park. These are rare, but present in both the upper and lower sampling horizons. Similar pollen was reported from the Miocene Palouse Falls locality of Washington, but not figured (Barnett & Fisk, 1980).

Poaceae. Several well-preserved grains of grass pollen (Fig. 11I) have been identified from all sample horizons at Vasa Park. This type is rare, but the presence of grasses at Vasa Park is corroborated by the phytolith analysis.

Potamogetonaceae. Rare pollen of *Potamogeton* L. (Fig. 11G) is present at Vasa Park.

Smilacaceae. *Smilax magna* Chaney (Fig. 6G). *Smilax magna* is preserved as rare examples at Vasa and was also present in the Middle Miocene Clarkia (Smiley & Rember, 1985), Mascall (Chaney and Axelrod, 1959), and Trout Creek (Graham, 1963) localities. It was also present in the Late Miocene Ellensburg Formation (Smiley, 1963). Chaney and Axelrod (1959) argued for designating all Northwest Miocene occurrences of *Smilax* L. by the epithet *magna* because species could not be reliably separated on leaf characters alone. The nearby Middle Eocene Puget Group deposits record the first known occurrence of *Smilax* in western Washington (Wolfe, 1968).

Typhaceae. Pollen monads of the *Typha* L./*Sparganium* L. type (Fig. 11H) are found from the upper sampling horizon at Vasa Park. No macrofossils have been found.

Angiosperms, Dicotyledons.

Altingiaceae. *Liquidambar* L. sp. (Fig. 12D). Pollen grains of *Liquidambar* occur rarely at the site. No macrofossils have been found. *Liquidambar* is a common element in the Middle Miocene floras of the Pacific Northwest, and today has disjunct distribution in Asia and eastern North America and Central America.

Aquifoliaceae. *Ilex* L. sp. (Fig. 12G). *Ilex* is uncommon, but found in all pollen samples. No macrofossils have been found.

Asteraceae. Uncommon but distinctive grains of pollen from the Asteraceae (Fig. 11N) are present in samples from the upper horizon.

Betulaceae. *Alnus* Mill. sp. (Fig. 7G, F). Common leaves and rare infructescences document the presence of *Alnus* at Vasa Park. Overlapping leaf morphologies preclude the separation of *Alnus* from *Betula* L. based on leaf characters alone. At Vasa Park the presence of *Alnus* reproductive structures and the overwhelming preponderance of *Alnus* over *Betula* pollen support an identification of *Alnus* for the leaves. The species *A. relata* (= *A. relatus* (Knowlton) Brown) is recorded from the nearby coeval Mashel Formation (Walters, 1964) and *Alnus* pollen was also recovered from the Hammer Bluff Formation in Renton (Mullineaux, 1970). *Alnus* is common in most Northwest deposits from the Early Eocene onwards, and five species occur today in Washington and Oregon (Franklin & Dyrness, 1988). The leaf characters of the Vasa Park *Alnus* correspond closely to modern *A. sinuata* (Regel) Rydb., which occurs in western Washington.

Several genera of Betulaceae are represented in the palynoflora, including *Alnus* (Fig. 11K), *Betula* (Fig. 11J), *Corylus* L. (not figured), and *Ostrya* Scop./*Carpinus* L. (not figured) type. *Alnus* is particularly abundant, represented by 4-, 5-, 6-, and 7-pore forms (the 4- and 5-pore forms are predominant). It comprises 4% of the pollen count in the lower sampling horizon, and up to 24% of the counts in the upper horizons, where it is a dominant type. The other genera of the Betulaceae are minor contributors to the overall palynoflora.

Cercidiphyllaceae. *Cercidiphyllum crenatum* (Unger) Brown (Fig. 6C). *Cercidiphyllum crenatum* is a common macrofossil species recovered at Vasa Park, as well as from the Middle Miocene in the Mascall Formation and at Clarkia (Chaney & Axelrod, 1959; Smiley & Rember, 1985). It is recorded from the Late Miocene Ellensburg Formation (Smiley, 1963) as well. Wolfe (1968) identified *C. piperoides* (Lesquereux) LaMotte from Middle Eocene Puget Group sediments in King County.

Rare grains of *Cercidiphyllum* Siebold & Zucc. type pollen (not figured) are found in the lower sampling horizon. These are consistent with modern pollen of *Cercidiphyllum*, and are similar to fossil pollen from the Miocene of Oregon identified as *Cercidiphyllum* by Gray (1958); however, the grains are folded and thus their identification is not certain.

Chenopodiaceae. Three pollen grains similar to that of the Chenopodiaceae (Fig. 11M) were identified from the Vasa Park palynoflora. Similar pollen has been reported from other Miocene sites in the Pacific Northwest (Chaney & Axelrod, 1959; Graham, 1965; Barnett & Fisk, 1980; Smiley & Rember, 1985). Graham (1965) notes that pollen of the Chenopodiaceae is morphologically similar to the Amaranthaceae and thus difficult to separate. Barnett and Fisk (1980) recorded their specimens as Chenopodiaceae, cf. *Sarcobatus* Nees. The Vasa Park specimens are small in size (20–25 μm), have relatively few pores, and bear a strong resemblance to modern *S. vermiculatus* (Hook.) Torr. It should be noted that *Sarcobatus* was removed from the Chenopodiaceae/Amaranthaceae clade and assigned to the monogeneric family Sarcobataceae by Behnke (1997). We refer to the Vasa Park pollen type as cf. Che-

nopodiaceae to allow comparison with the previously described palynofloras in Table 2.

Ericaceae. Rare tetrads of ericaceous pollen (Fig. 12K) were found in sample UWBM PB22772. These were not detected in any other samples.

Fagaceae. *Fagus washoensis* LaMotte (Fig. 6D). Common leaves at Vasa Park match the characters of *F. washoensis*. This species was recorded in the Middle Miocene Mascall Formation (Chaney & Axelrod, 1959), at Trout and Sucker creeks (Graham, 1963), and *Fagus* L. also occurs at Clarkia (Smiley & Rember, 1985). The species is also recorded in Late Miocene deposits of the Ellensburg Formation (Smiley, 1963) and the nearby coeval Hammer Bluff Formation (Mullineaux, 1970).

The Fagaceae is also represented in the pollen assemblage by cf. *Castanea* Mill., *Fagus* sp., and two types of *Quercus* L. The *Castanea* type (not figured) is only represented by a few pollen grains. *Fagus* (Fig. 12J) and *Quercus* (Fig. 12H) are more common, especially from the lowest sampling horizon.

Hydrangeaceae. *Hydrangea bendirei* (Ward) Knowlton (Fig. 7D). Several well-preserved leaves of *Hydrangea* L. have been found at Vasa Park. The species was widespread in the Middle Miocene, occurring in the Latah (Knowlton, 1926; Brown, 1936), Mascall (Knowlton, 1902; Chaney & Axelrod, 1959), and Trout Creek and Sucker Creek (Graham, 1963) deposits.

Juglandaceae. The Juglandaceae is represented by pollen of *Carya* Nutt. (Fig. 12A), *Juglans* L. (Fig. 12C), and *Pterocarya* Kunth (Fig. 12B). *Juglans* is quite rare, with only two pollen grains found in the 16 slides examined for this study. *Carya* and *Pterocarya* are more common, but still compose less than 1% of the pollen in all of the samples that were counted. All three of these taxa are commonly reported in the palynofloras of the Pacific Northwest.

Lauraceae. *Persea pseudocarolinensis* Lesquereux (Fig. 6E). *Persea pseudocarolinensis* was a widespread species first recorded in King County from the Middle Eocene Puget Group (Wolfe, 1968). This species is also found at all of the well-known Northwest Middle Miocene localities and the Late Miocene Ellensburg flora (Smiley, 1963). *Persea lanceolata* (Berry) Brown was identified by Wolfe (Walters, 1964) from the nearby coeval Mashel Formation, but no description or figure was provided. That species was separated from *P. pseudocarolinensis* based on a narrow-leaved morphotype of *Persea* found in the Latah flora.

Magnoliaceae. Only two pollen grains of the Magnoliaceae (not figured) have been identified from Vasa Park. No macrofossils have been identified.

Malvaceae. Cf. *Gossypium* L. sp. (Fig. 6F). Common leaves at Vasa Park have morphology similar to modern *G. barbadense* L. In both cases, leaves are palmate, 3- to 5-lobed, entire, lobes with acuminate tips, actinodromous with an obtuse to reflex cordate base, brochidodromous secondaries, percurrent tertiaries, and an irregular reticulate fabric. Gossypol glands observable on modern leaves are possibly present in the fossil but equivocal. The stellate hairs present on modern *Gossypium* leaves are not observed in the fossil. Graham (1963) described *G. arnoldii* Graham from Trout Creek based on leaf morphology, but no other *Gossypium* fossils have been described prior to the Pleistocene. The genus *Gossypium* has been estimated to have originated approximately 12.5 Ma (Wendel et al., 2010).

Nyssaceae. *Nyssa* L. pollen (Fig. 12L) is present but rare at Vasa Park. This genus was widespread in the Pacific Northwest during the Miocene.

Oleaceae. Rare examples of *Fraxinus* L. pollen (Fig. 12I) are present in the Vasa Park assemblage. No macrofossils have been found.

Onagraceae. Only two grains of distinctive pollen (not figured) from the Onagraceae were noted at Vasa Park; both were from the upper sample horizon.

Platanaceae. *Platanus dissecta* Lesquereux (Fig. 7A, B). This widespread species has been found in the Northwest Middle Miocene at Clarkia

TABLE 2. Vasa Park palynoflora compared to selected Middle Miocene localities.

Family	Genus	Vasa Park 11.4 Ma	Palouse Falls[1] 15.5 Ma	Clarkia[2,3] 15–15.5 Ma	Sucker Creek[4,5] 14.8–16 Ma[6]
Lycopodiaceae	*Lycopodium*	×	×	×	×
Selaginellaceae	*Selaginella*	×	×		
Equisetaceae	*Equisetum*	x?	×		×
Azollaceae	*Azolla*		×		
Blechnaceae	*Woodwardia*				×
Davalliaceae	*Davallia*				×
Dryopteridaceae	undetermined	×			
Osmundaceae	*Osmunda*				×
Polypodiaceae	undetermined	×	×	×	×
Cupressaceae	*Sequoia/Metasequoia*	×			x?
Gnetaceae	*Ephedra*				×
Pinaceae	*Abies*	×	×	×	×
	Cedrus type	×	×	×	×
	cf. *Keteleeria*			×	×
	Picea	×	×	×	×
	Pinus	×	×	×	×
	Pseudotsuga/Larix	×	×	x?	x?
	Tsuga	×	×	×	×
Taxodiaceae-Cupressaceae-Taxaceae	TCT	×	×	×	×
Incertae sedis	Podocarpaceae/*Cathaya*	×	×		×
Liliaceae	undetermined	×	×		
Poaceae	undetermined	×	×		×
Potamogetonaceae	*Potamogeton*	×	×		×
Typhaceae	*Typha/Sparganium* (monad)	×	×	x?	×
Altingiaceae	*Liquidambar*	×	×	×	×
Anacardiaceae	*Rhus*			×	
Apiaceae	undetermined				×
Aquifoliaceae	*Ilex*	×	×	×	×
Asteraceae	undetermined	×			×
Berberidaceae	*Mahonia*				×
Betulaceae	*Alnus*	×	×	×	×
	Betula	×	×	×	×
	Corylus	×	×	×	×
	Ostrya/Carpinus	×	×	x?	×
Buxaceae	*Pachysandra*				×
Caprifoliaceae	undetermined				×
Cercidiphyllaceae	cf. *Cercidiphyllum*	×			
cf. Chenopodiaceae	undetermined	×	×	×	×
Coriariaceae	undetermined		×		
Cornaceae	*Alangium*				×
	Cornus				×

TABLE 2. (*continued*)

Family	Genus	Vasa Park 11.4 Ma	Palouse Falls[1] 15.5 Ma	Clarkia[2,3] 15–15.5 Ma	Sucker Creek[4,5] 14.8–16 Ma[6]
Elaeagnaceae	*Shepherdia/Elaeagnus*			×	×
Ericaceae	undetermined	×	×	×	×
Fabaceae	undetermined				×
Fagaceae	cf. *Castanea*	×		x?	×
	Fagus	×	×	×	×
	Lithocarpus				×
	Quercus	×	×	×	×
Hippocastanaceae	*Aesculus*			×	
Juglandaceae	*Carya*	×	×	×	×
	Engelhardtia type			x?	
	Juglans	×	×	×	×
	Pterocarya	×	×	×	×
Lamiaceae	undetermined		×		
Magnoliaceae	undetermined	×			
	Liriodendron			×	
	Magnolia			×	
Malvaceae	undetermined		×		×
	Tilia		×	×	×
Moraceae	*Morus*		×		
Myricaceae	*Myrica*			×	
Nymphaceae	*Nymphaea polymorpha*		×		×
Nyssaceae	*Nyssa*	×	×	×	×
Oleaceae	*Fraxinus*	×	×		×
Onagraceae	undetermined	×	×		×
Platanaceae	*Platanus*	×	×	×	×
Polygonaceae	cf. *Polygonum*		×		
Rhamnaceae	undetermined			×	
Rosaceae	undetermined			×	×
Salicaceae	*Populus*	x?	×		×
	Salix	×	×		×
Sapindaceae	*Acer*	×	×	×	×
Theaceae	undetermined		×		
Ulmaceae	*Celtis*		×	×	×
	Ulmus/Zelkova	×	×	x?	×
Vitaceae	cf. *Parthenocissus*			×	

[1] Barnett & Fisk (1980).
[2] Smiley & Rember (1985).
[3] Gray (1985).
[4] Graham (1965).
[5] Fields (1996).
[6] Graham (1965) reports a date of 16.7 Ma for the Sucker Creek Formation. Fields (1996) suggests a younger date of 14.8–16 Ma based on newer Ar/Ar dates and geologic evidence. We accept Fields' date for the purpose of this comparison.

(Smiley & Rember, 1985), Mascall (Chaney & Axelrod, 1959), Sucker and Trout creeks (Graham, 1965), and in the Late Miocene Ellensburg Formation (Smiley, 1963). The species was also recorded in the nearby coeval Mashel Formation (Walters, 1964), and Wolfe (1968) included *Platanus* L. in the flora of the Middle Eocene Puget Group in King County. *Platanus* pollen is a rare constituent of the Vasa Park palynoflora.

Salicaceae. This family is represented by pollen of *Salix* L. (Fig. 12E) and possibly *Populus* L. (not figured). *Salix* pollen is relatively common, making up slightly over 1% of the assemblage in each sample that was counted. The cf. *Populus* pollen is rare, with only two grains identified. Gray (1985) notes that *Populus* pollen has low preservation potential, and thus its presence in the fossil record is sporadic.

Sapindaceae. *Acer* L. (Fig. 6A, B). Well-preserved leaves and samaras of *Acer* are common at Vasa Park. The leaves range widely in size from a laminar length of 5–20 cm. They are shallowly lobate, 3- or 5-lobed, with a finely serrate margin. The leaves most closely resemble *A. glabroides* Brown, although *A. glabroides* is usually 3-lobed. The samaras found at Vasa Park do not match those associated with *A. glabroides* by previous authors (Brown, 1936; Wolfe & Tanai, 1987). The samaras found at Vasa closely resemble samaras of *A. medianum* Knowlton. Wolfe and Tanai (1987) argued for an association between samaras of *A. medianum* and leaves of *A. columbianum* Chaney & Axelrod based on the co-occurence of leaves of *A. columbianum* with samaras of *A. medianum* at eight of the 14 known localities where *A. medianum* samaras occur. But *A. glabroides* is also found at many of the same localities.

Multiple species of *Acer* are present at each of the Middle Miocene localities of the Pacific Northwest (Knowlton, 1902, 1926; Brown, 1936; Chaney & Axelrod, 1959; Graham, 1963; Smiley & Rember, 1985). In many cases the actual number of species is overstated because isolated leaves and samaras cannot be reliably associated with each other. *Acer* was also found at both of the coeval western Washington Late Miocene localities of the Mashel and Hammer Bluff formations (Walters, 1964; Mullineaux, 1970).

Two types of *Acer* pollen (Fig. 12F) are also found at Vasa Park, although they are both rare.

Aesculus L. sp. (Fig. 7C, E). A few leaflets of *Aesculus* have been found at Vasa Park. *Aesculus* has also been identified at Clarkia (Smiley & Rember, 1985) but has not been recognized at other Pacific Northwest Miocene localities.

Scrophulariaceae. *Paulownia columbiana* Smiley (Fig. 7H). Distinctive palmate leaves with prominent tertiaries and a round to obtuse apex were described as *P. columbiana* by Smiley (1961) from the Late Miocene Ellensburg Formation and compared to extant *P. tomentosa* (Thunb.) Steud. *Paulownia tomentosa* has a wider range of leaf morphologies, including lobed leaves, while *P. columbiana* leaves are not lobed. Unlobed leaves of *P. tomentosa* and *P. columbiana* are entire, except for a few small teeth found near the leaf base. Excellent examples have been collected at Vasa Park. *Paulownia* Siebold & Zucc. is also found in the Middle Miocene at Clarkia (Smiley & Rember, 1985), and Knowlton (1926) figured a Latah specimen as *Acer* (plate XXVIII, fig. 1) that likely represents this taxon. He also illustrates a *Paulownia* capsule (plate XXIX, fig. 12) that he described as *Carpites paulownia* Knowlton. *Paulownia columbiana* was also identified by Wolfe in the coeval Mashel Formation (Walters, 1964). Wolfe figures a leaf with the same characteristics from the Puget Group (Wolfe, 1968: plate 5, fig. 1) which he described as *Macaranga pugetensis*.

Ulmaceae. *Ulmus speciosa* Newberry (not figured). *Ulmus* L. is another widespread genus found at most of the Middle and Late Miocene localities in the Pacific Northwest. Knowlton (1926) included *U. speciosa* in the Latah flora, and Chaney and Axelrod (1959) also identified it in the Mascall flora, but described a second species, *U. paucidentata*, based on smaller leaf size

and slender shape. That species was included in the Ellensburg Formation flora (Smiley, 1963), but the specimens at Vasa correspond best with the description of *U. speciosa*. This species was reported by Wolfe in the coeval Mashel Formation (Walters, 1964). *Ulmus* was also reported from the nearby Late Miocene Hammer Bluff Formation (Mullineaux, 1970). *Ulmus oregoniana* Knowlton was recognized in the Middle Eocene Puget Group flora (Wolfe, 1968). Ulmaceous pollen (Fig. 11L) has been found in 4-, 5-, and 6-pored forms, although it is rare.

POLLEN RESULTS

The pollen in the three counted samples was generally abundant and well preserved. In the interest of showing the most significant aspects of the palynoflora, the pollen diagram (Fig. 8) presents only those taxa that contributed at least 1% of the total counts. Conifer pollen is dominant in all samples, with TCT being the major contributor. *Pinus* also makes a strong showing, and *Tsuga* is important from the layers near the top of the exposure. Among angiosperms, *Alnus* is by far the major contributor, and is the single most common palynomorph in sample UWBM no. PB22772. Pteridophytes are an important constituent of all samples, making up approximately 8%–10% of the total counts. One aspect of the flora that is not clear from the pollen diagram is the high species richness in all three samples. We were able to distinguish over 100 distinct palynomorphs, with high species richness in all groups: pteridophytes, conifers, and angiosperms. Those types that were identifiable to the family or genus level are presented in Table 2.

Because the macroflora assemblage was not sufficiently well preserved or diverse to allow a climate estimate based on techniques using nearest living relatives or leaf morphology, we used the coexistence approach (Mosbruger & Utescher, 1997) based on the fossil pollen assemblage. Pollen is adequate but not ideal for this purpose, since the coexistence approach works best with fossils identified to the genus or species level. This allows for a better determination of possible nearest living relatives for a given fossil taxon and thus tighter constraints on the paleoclimate estimates. Since pollen is typically only identified at the family or genus level, the climatic resolution provided by the analysis is lower. The results of the coexistence analysis are as follows:

Mean annual temperature: 11.6°C–16.6°C
Cold month mean temperature: –0.3°C–2.9°C
Warm month mean temperature: 23.0°C–25.7°C
Mean annual precipitation: 641–1577 mm
Wet month precipitation: 116–245 mm
Dry month precipitation: 8–41 mm
Warmest month precipitation: 89–175 mm

PHYTOLITH RESULTS

The extracted phytolith assemblages were deemed well preserved, due to the presence of fine ornamentation on the grass silica short cells and the generally unaltered texture of the phytoliths, despite some etching of larger bodies, and thus considered appropriate for quantitative phytolith analysis (Strömberg, 2003; Strömberg et al. 2007b). Although sample UWBM no. PB22779 had relatively low phytolith productivity, UWBM nos. PB22778 and PB22780 had extremely low productivity (13 slides had to be examined to achieve a sufficient count).

UWBM no. PB22778 has a relatively high abundance of FI-t phytoliths at 57% (95% CI: 52%–63%), including anticlinal epidermal cells, helical tracheary elements, and nodular bodies. A single palm phytolith was also noted, as well as rare sedge forms. UWBM no. PB22779 has a very high FI-t ratio (94%; 95% CI: 92%–96%), and contained forms such as nodular bodies and polyhedral epidermis, as well as a single palm phytolith. Similarly, UWBM no. PB22780 has a high FI-t ratio (94%; 95% CI: 91%–98%), with FI-TOT forms made up primarily by nodular bodies.

TABLE 3. Vasa Park macroflora compared to selected Northwest Miocene localities and the Middle Eocene Puget Group floras.

Vasa Park	Tyrrell PA 19[1]	Latah[2]	Mascall[3]	Sucker/Trout Creek[4]	Clarkia[5]	Puget[6]
Equisetae						
Equisetum sp.		*	*	*Equisetum miocenicum*		
Pteridophytae						
Allantodiopsis sp.						*Allantodiopsis pugetensis*
Woodwardia sp.				*Woodwardia deflexipinna*		
Gymnospermae						
Chamaecyparis linquaefolia				*Chamaecyparis linguaefolia*	*Chamaecyparis* sp.	
Angiospermae						
Acer sp.	*Acer tyrrellii*	*Acer* (4 spp.)	*Acer* (6 spp.)	*Acer* (7 spp.)	*Acer* sp.	
cf. *Gossypium* sp.				*Gossypium arnoldii*		
Platanus dissecta	*Platanus dissecta*		*Platanus dissecta*	*Platanus dissecta*	*Platanus* sp.	*Platanus* sp.
Paulownia sp.	*Paulownia columbiana*	*Carpites paulownia*, "*Acer*" L.?			*Paulownia* sp.	*Macaranga pugetensis*
Hydrangea bendirei		*Hydrangea bendirei*	*Hydrangea bendire*	*Hydrangea bendire*	*Hydrangea* sp.	
Fagus washoensis	**		*Fagus washoensis/ idahoensis*	*Fagus washoensis*	*Fagus/Pseudofagus*	
Cercidiphyllum crenatum	**		*Cercidiphyllum crenatum*		*Cercidiphyllum* sp.	*Cercidiphyllum peperoides*
Smilax magna	**		*Smilax magna/warda*	*Smilax magna*	*Smilax* sp.	*Smilax* sp.
Alnus sp.	*Alnus rubrius*	*Alnus, Betula* (8 spp.)	*Alnus, Betula* (4 spp.)	*Alnus, Betula* (6 spp.)	*Alnus, Betula*	*Alnus* (3 spp.)
Persea pseudocarolinensis	*Persea pseudocarolinensis*	*Persea lanceolata*	*Persea pseudocarolinensis*	*Persea pseudocarolinensis*	*Persea* sp.	*Persea pseudocarolinensis*
Ampelos sp.					*Ampelos* sp.	
Ulmus speciosa	*Ulmus paucidentata*	*Ulmus speciosa*	*Ulmus speciosa/ paucidentata*	*Ulmus speciosa/ paucidentata*	*Ulmus*	*Ulmus oregoniana*

Abbreviations: L. = Leaf
* Reported but discredited
** Occur at other Ellensburg Formation localities.
[1] Ellensburg flora (Smiley, 1963)
[2] Flora of the Latah Formation (Knowlton, 1925; Brown, 1936)
[3] Miocene flora of the Columbia Plateau (Chaney & Axelrod, 1959)
[4] Sucker Creek and Trout Creek Miocene floras of southeastern Oregon (Gruner, 1963)
[5] Miocene Clarkia flora (Smiley & Rember, 1985)
[6] Paleogene biostratigraphy of nonmarine rocks in King County, Washington (Wolfe, 1968)

is relatively rare, whereas the remainder contribute a small but significant percentage of the pollen in each sample. Coniferous pollen is often interpreted as a slope or montane element (e.g., Chaney & Axelrod, 1959; Smiley & Rember, 1985), but it should be noted that *Abies, Picea, Pinus, Pseudotsuga, Thuja* L., and *Tsuga* are all present in the extant coastal lowland forests of the Pacific Northwest, as well as at higher elevations.

The abundance of *Alnus* pollen suggests a local source. Modern *Alnus* is a common riparian tree type and a pioneer species in disturbed habitats. The relative abundance of fern spores can also be associated with disturbance (Walker & Sharpe, 2010), and *Salix* is a common riparian shrub, while *Nyssa* is associated with swamps and wetlands. The macrofossil records of abundant ferns and pioneer angiosperms such *Alnus* and *Acer*, coupled with evidence provided by the palynoflora, are consistent with a disturbance or early successional flora that formed in a fluvial, floodplain environment. The presence of fine siltstone sediments and aquatic taxa such as *Typha/Sparganium* and *Potamogeton* in the pollen record indicate that there were also some quiet water areas in the vicinity.

Table 2 shows a comparison of the Vasa Park palynoflora with several other Miocene sites from the Pacific Northwest. Even though these sites span a distance of hundreds of kilometers and a time period of several million years, the similarities are striking. Of the 64 total taxa listed in the table, 36% are common to all of the floras and 51% are found in at least three out of four floras, indicating that there was a widespread and stable regional forest assemblage during the Miocene. Vasa Park occurred during the global cooldown that followed the Mid-Miocene Climatic Optimum (Zachos et al., 2001), but it is clear that no significant floral turnover had yet occurred in the Pacific Northwest by this time.

Fifty percent of the genera found at Vasa Park are no longer extant in northwest North America. They are found in eastern North American and Eurasian forests with a temperate climate and year-round rainfall. The coexistence approach analysis suggests a similar climate at Vasa Park during the Miocene, with the mean annual temperature in a range of 11.6°C–16.6°C, limited frost in the winter (cold month mean temperature, –0.3°C to 2.9°C), moderate to high precipitation (mean annual precipitation, 641–1577 mm), and adequate rainfall during the growing season (warm month precipitation, 89–175 mm). This is consistent with climate interpretations for other Miocene floras from the Northwest, and the Vasa Park climate analysis, coupled with the high degree of taxonomic overlap between the Miocene palynofloras, supports the hypothesis that the regional climate did not change significantly during the 4- to 5-million-year time frame represented by these floras. Graham (1999) uses evidence from a number of fossil sites in the western United States to show that a cooling climate and dry summer conditions started to set in after the Mid-Miocene Climatic Optimum, beginning in southwestern North America and the continental interior. The dry summer conditions would have resulted in the loss of many deciduous hardwoods that require adequate summer rainfall. According to this analysis and consistent with our data, the Pacific Northwest did not experience these effects until later, and Graham (1999) states that the warm temperature and wet summer climate conditions persisted in the region into the Early Pliocene.

Because the phytolith assemblages were generally well preserved in Vasa Park deposits, we assume that they reflect deposition from plants growing on the floodplain, rather than phytoliths transported by water or wind from surrounding highlands (Osterrieth et al., 2009). The overall low abundances of sedge phytoliths and other biosilica (e.g., diatoms, sponge spicules) commonly associated with lakes and rivers further indicate that the assemblages represent deposition in a soil, rather than in water, such as in an oxbow lake. All extracted samples from Vasa Park had very low

concentrations of phytoliths compared to typical Cenozoic sediments (Strömberg, unpublished data). This suggests that the horizons collected, even those that had clear root traces, did not remain stable soil surfaces for very long. Of the three samples that were quantitatively analyzed for phytoliths, UWBM nos. PB22779 and PB22780 both point to closed habitats (forest) with a low abundance of PACMAD grasses and rare pooids. Since these samples were collected from the same horizon, their similarity indicates little spatial heterogeneity in vegetation, at least over the small distance sampled at Vasa Park. The higher abundance of sedges in UWBM no. PB22779 suggests that this sample reflects a microhabitat closer to water. Assemblage UWBM no. PB22778 appears to represent a somewhat more open microhabitat, with a mix of trees and forbs, mainly PACMAD grasses and infrequent pooids. The presence of palm phytoliths in two assemblages opens up the intriguing possibility that palms persisted in the Pacific Northwest until the early Late Miocene; the youngest previously described palms from the region are pollen from the Middle Miocene Succor Creek flora of the Oregon-Idaho border (Taggart & Cross, 1990), and phytoliths from the late Middle and early Late Miocene of southwestern Montana (Strömberg, 2005; Smith et al., 2012; Strömberg et al., 2012). In addition, palm phytoliths have been recovered from the Middle Miocene Mascall Formation of Oregon (R. Dunn & C. Strömberg, unpublished data). However, because of the very low abundance of palm phytoliths at Vasa Park, the fact that other monocotyledons produce phytoliths that can look similar to palm phytoliths (e.g., orchids; Piperno, 1988), and the lack of co-occurring pollen attributable to Arecaceae, the identification of palms at Vasa Park has to remain tentative.

In all, phytolith assemblages point to a mostly forested floodplain at Vasa Park. The abundance of PACMADs in grass communities could be consistent with warmer climates, and could also point to mesophytic PACMAD grasses growing close to water (e.g., *Arundo* L.; see Strömberg et al., 2007a). The specific PACMAD morphotypes that dominate GSSC assemblages (e.g., so-called almost panicoid bilobates) are similar to those produced by *Arundo*. However, as noted above, other lines of evidence (diatoms, etc.; Fig. 9) are not congruent with an interpretation of these assemblages as mirroring wetland vegetation. Palms, if present, would also support the pollen-based inference that climate was warmer than today in Washington during the early Late Miocene. This reconstructed vegetation differs from roughly coeval phytolith assemblages from sites further inland, in western Montana. Here, assemblages appear to reflect open habitats dominated by cool-temperate pooids (Strömberg et al., 2012). Similarly, faunal and paleosols data have been interpreted as pointing to savanna or woodland habitats for the early Late Miocene of eastern Oregon (Shotwell, 1970; Retallack, 2004). These differences may be a result of a difference in regional climate (e.g., rainfall) between western Washington and areas further east, but it cannot be ruled out that it is a consequence of sampling different, local edaphic conditions.

CONCLUSIONS

Applying a range of geological and paleobotanical approaches, we are able to more completely describe the flora recorded at Vasa Park than by using single lines of evidence. Geological study not only provides a "big picture" view of the sedimentary system that created the deposit but also informs us about taphonomic filtering and the age of fossil-bearing sediments. The macroflora mostly records localized plant communities adapted to regular disturbance close to fluvial channels and is not diverse enough to estimate climate. The palynoflora adds a regional perspective of likely conifer-dominated upland floras and the much more species-rich surrounding hardwood forests. It also provides us with a regional climate estimate. The phytolith assemblage informs us about

forest coverage and grass ecology in the flora recorded at Vasa Park. In all, these lines of evidence indicate that plant communities in western Washington differed little from Middle to Late Miocene floras from around the Pacific Northwest, and that the regional climate had remained mild and humid since the Middle Miocene. Unlike coeval sites from the northern Rocky Mountains and Great Plains, open habitats dominated by cool- and dry-adapted pooid grasses appear not to have been important in the Pacific Northwest during this time. These patterns suggest that the Pacific Northwest may have served as a climatic refugium amidst dropping global temperatures and increasing seasonality during the Late Miocene (Zachos et al., 2001).

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CONNECTIVITY DYNAMICS SINCE THE LAST GLACIAL MAXIMUM IN THE NORTHERN ANDES: A POLLEN-DRIVEN FRAMEWORK TO ASSESS POTENTIAL MIGRATION

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ABSTRACT

We provide an innovative pollen-driven connectivity framework of the dynamic altitudinal distribution of North Andean biomes since the Last Glacial Maximum (LGM). Altitudinally changing biome distributions reconstructed from a pollen record from Lake La Cocha (2780 m) are assessed in terms of their changing surface and connectivity within the study area. The upper forest line (UFL) ecotone lodged during much of the time around 2000 m (LGM), 2400 m (ca. 14–8 ka), 2800 m (ca. 8–3 ka), and 3550–3600 m (modern time). This resulted in a four-fold increase of the area covered by mountain forest (Andean and sub-Andean), a decrease of 96% of páramo, and a disappearance of permanent snow. Upslope migration of the UFL of 20 vertical m yr^{-1} and more, as inferred from the pollen record, was spatially assessed: reduced surface area, dispersal limitation, reduced connectivity, and extirpation of the subpáramo biome during a few centuries is shown. The study area includes abundant higher mid-range altitudes (2600–3400 m), with a steep reduction of available surface area and increased dispersal distance in the high and low altitudes. In this range, each 100-m altitudinal rise of the UFL results in 20%–60% reduction of the surface area available for páramo and connectivity. The critical elevations where large biome surfaces start to disconnect depend on the elevation of lowest thresholds in the landscape and the elevation of summits. The 2500–3600 m elevation range is most dynamic in terms of geography and ecological species sorting; the 1000–1500 m interval is relatively stable and is permanently covered by Andean forest, making this interval less sensitive for monitoring climate change. When forests migrate to higher elevations, distribution nuclei of species are compressed, resulting temporarily in a higher species diversity. The species dissimilarity coefficient reflects rate of (ecological) change more adequately than the rate of palynological turnover, because the latter is much influenced by the lengths of the time steps between the pollen samples. Spatial analysis of site-specific dynamics provides exciting new insights into past vegetation dynamics, with potential for better understanding species-area distributions, distribution patterns of biodiversity, and conservation of mountain ecosystems.

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Key words: Andean biome dynamics, elevational distribution patterns, GIS, landscape connectivity, Last Glacial Maximum, palynological turnover rate, upper forest line.

Landscape connectivity is considered a key issue for the maintenance of natural ecosystem stability and integrity (Saunders et al., 1991; Taylor et al., 1993; Collinge, 1998; With & King, 1999). The ability of species to survive is reduced by habitat loss, as well as by fragmentation of patches, since disconnections prevent recolonization (Fahrig, 2003; Foley et al., 2005). Therefore, the total available surface of a biome and its landscape connectivity are relevant to understanding the pressure on populations and species, i.e., survival of the gene pool.

Altitudinally shifting boundaries of montane biomes intrinsically mean changing degrees of connectivity (Ramírez-Barahona & Eguiarte, 2013). The present altitudinal distribution of biomes in the northern Andes is a "frozen" moment after a long series of Pleistocene changes, mainly driven by climate change (Bogotá-Angel et al., 2011; Torres et al., 2013). In the northern Andes biome responses to climate change have been captured in the dense network of palynologically studied sediment cores (e.g., Marchant et al., 2009; Grimm et al., 2013). In pollen-based studies of past vegetation change, pollen taxa are classified into ecologically meaningful groups, reflecting main biomes. Then, past altitudinally changing ranges of biomes are inferred from changing proportions of these ecological groups in the pollen spectra. Hooghiemstra and Van der Hammen (2004) compared altitudinal biome distributions of the Last Glacial Maximum (LGM) in the Colombian Andes with the present day and provided first estimates of surface variability of the biomes through time. However, distributional dynamics of shifting biome boundaries in montane regions in terms of available habitat surface and landscape connectivity have not been addressed so far.

The landscape relief poses restrictions on habitat availability, connectivity, and dispersal patterns. Certain biomes and species are ecologically limited to the highest mountain ranges, such as the páramo vegetation in the northern Andes (Van der Hammen & Cleef, 1986; Luteyn, 1999). The importance of understanding species dispersal in relation to landscape connectivity was recently stressed by several fine-resolution pollen records, showing very fast upslope shifts of ecotones, such as the upper forest line (UFL), for example, in the Colombian pollen records of Lake Fúquene at 2540 m (Groot et al., 2011, 2013), Lake La Cocha at 2780 m (González-Carranza et al., 2012), and in the pollen record of Llano Grande at 3460 m (Velásquez-Ruiz & Hooghiemstra, 2013). These records showed that forest may shift significantly faster upslope than subpáramo shrub, resulting in a temporary loss of the overruled biome. In such cases, a high connectivity, with areas where isolated populations were conserved, is crucial for a rapid return of the extirpated biome (Pearson, 2006). These dynamic patterns can be better understood by analyzing biome and species distributions in a landscape perspective.

The objective of this study is to assess changes in connectivity of altitudinally distributed biomes in the northern Andes in terms of biome surface and migration potential. We make the step from a single-site view on the altitudinal distribution of biomes to a spatially integrated view of biome connectivity. Our analysis is driven by past environmental conditions inferred from pollen record La Cocha-1 (González-Carranza et al., 2012). We selected an area including the lake and showing the full elevational range from Amazonian lowland to the nearest mountaintops. Our connectivity assessment is focused in particular on the effect of the altitudinally shifting UFL on the habitat surface area and the connectivity of páramo biome patches. Results of this case study improve our understanding of how biomes in montane regions of the northern Andes respond to climate change in surface and connectivity. Implications

for scenarios of potential future developments are discussed.

SETTINGS OF THE STUDY AREA

CURRENT CONDITIONS AND LANDSCAPE

The selected study area is located in the Guamuez basin in the Eastern Cordillera of Colombia and covers a total area of 7559 km^2 (Fig. 1). The study area is found between 0°45′N and 1°30′N and between 76°44′W and 77°33′W, and elevations range from 300 to 4207 m.s.m. Toward the east the basin faces the Amazonian lowlands. Precipitation in the study area originates mainly from the Atlantic Ocean, and amounts are influenced by changes in the intensity of trans-Amazonian moisture transport (Gan et al., 2004). The typical wind patterns of this region are dominated by the trade winds blowing from the northeast, leading to enhanced precipitation on the eastern flank of the Andes. Mean annual precipitation (MAP) near Lake La Cocha is 1400 mm (Van Boxel et al., 2013), with values between 1300 and 2000 mm for most of the study area (Hernandez et al., 2004). Most precipitation falls between April and August, and it is lowest in December. Toward the west, dry inter-Andean high plains lie in the rain shadow and have a MAP of 700–1400 mm. Lake La Cocha (1°05′N, 77°09′W) is located at an elevation of 2780 m.s.m. and is directly surrounded by steep slopes that reach up to 3600 m. At the elevation of the lake (2780 m), the mean annual temperature (MAT) is 11.6°C (Wetlands International, 2007), which is ca. 1.5°C less than expected in relation to its elevation (Van Boxel et al., 2013). With a surface of 41 km^2, Lake La Cocha is one of the largest lakes in the northern Andes.

MODERN VEGETATION

The altitudinal vegetation distribution of the northern Andes was studied by Van der Hammen (1974), Cleef and Hooghiemstra (1984), and Van der Hammen and Cleef (1986) (Table 1), among others. For the vegetation around Lake La Cocha we refer to González-Carranza et al. (2012), and here we present a general characterization appropriate to the aims of this study. The lake is surrounded by reed swamp. The lower parts of the slopes, once forested, are now covered by agricultural fields and pasture. Under natural conditions the slopes are covered up to 3550 m by Andean forest. Above this ecotone, reflecting the UFL, open páramo vegetation reaches to the summits. In the páramo small patches of forest dominated by *Polylepis* Ruiz & Pav. and *Gynoxis* Rchb. occur in protected areas (Van't Veer &

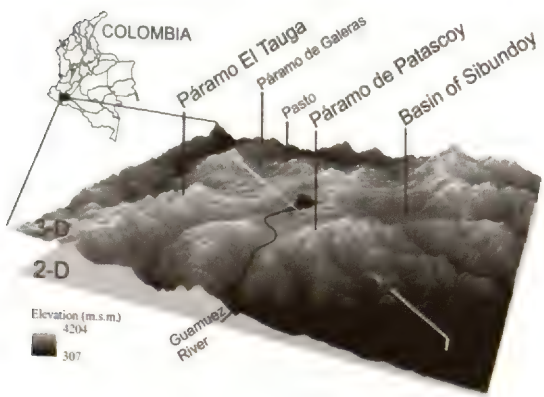

FIGURE 1. Relief map in 3-D of the study area in the south Colombian Andes, including Lake La Cocha at 2780 m elevation. The white line indicates the direction of the altitudina profile shown as the background of Figure 7. Most important geographical references in the region are signposted, such as the páramos and the city of Pasto. A vertical exaggeration factor of 2.5 was applied to the digital elevation model.

TABLE 1. Characterization of the present-day altitudinally organized biomes of the surroundings of Lake La Cocha.

Biome	Elevation (m.s.m.)	Characteristic taxa in pollen records	Mean annual temperature (MAT)
Grasspáramo	~3700–4200	Graminaceous genera *Agrostis* L., *Calamagrostis* Adans., *Festuca* L., *Muehlenbergia* Schreb., and *Swallenochloa* McClure; stem rosettes of *Espeletia* Mutis ex Bonpl. (Asteraceae); and herbaceous genera *Gentiana* L., *Halenia* Borkh., *Valeriana* L., and *Aragoa* Kunth.	8°C–4°C
Subpáramo	~3600–3700	dwarf forest and shrub of Asteraceae, Ericaceae, *Polylepis* Ruiz & Pav., *Escallonia* Mutis ex L. f., Hypericum L.	10°C–8°C
	~3550–3600	***UPPER FOREST LINE***	***~9.5°C***
Andean forest	~2300–3600	*Weinmannia* L., *Alnus* Mill., *Myrica* L., *Styloceras* Kunth ex A. Juss., *Podocarpus* L'Hér. ex Pers., *Clusia* L., *Myrsine* L., *Juglans* L., *Ilex* L., *Hedyosmum* Sw.	16°C–10°C
Sub-Andean forest	~1000–2300	*Acalypha* L., *Alchornea* Sw., *Cecropia* Loefl., *Arecaceae*, *Hieronima* Allem., *Ficus* L., Malpighiaceae	23°C–16°C

Hooghiemstra, 2000; Bakker et al., 2008). Human impact on the vegetation started at selected places in Colombia by the mid-Holocene time (Marchant et al., 2001). The pollen record of Lake La Cocha shows sudden and significant deforestation 1405 calibrated years before AD 1950 (cal yr BP).

UPPER FOREST LINE AND BIOME BOUNDARIES

In the present study, the altitudinal position of the UFL is pivotal. There is much debate on the natural (undisturbed) altitudinal position of the UFL (Wille et al., 2002; Bakker et al., 2008; Moscol-Olivera & Hooghiemstra, 2010; Jansen et al., 2013). Another relevant field of debate concerns the question of how plant associations shift altitudinally. Gleason (1926) observed that species are individualistically distributed along omnipresent environmental gradients and thus cannot form bounded communities. Gleason and many of his followers were of the opinion that plant species could not form integrated communities (plant associations and biomes) because of their individualistic behavior, and they criticized the community concept of Clements (1916) and Braun-Blanquet (1921). This debate is well presented in Van der Maarel (1975), Fernández-Palacios and de Nicolás (1995), Vázquez and Givnish (1998), and Nicolson and McIntosh (2002), among others, and critically analyzed by Shipley and Keddy (1987). Though Gleason and Clements held some contrasting views, they are not as incompatible as generally assumed (Nicolson & McIntosh, 2002; Jackson, 2006). In the present study we used the following assumptions: (1) the transition from continuous closed forest to open páramo vegetation reflects the natural UFL; (2) Andean forest and páramo are primarily climatologically constrained plant associations (biomes), but we do not exclude processes of interspecies competition. We support the working hypothesis that community structure depends on the local circumstances (Bader & Ruijten, 2008), the stage of the migration process (González-Carranza et al., 2012), and the degree of change (Van Nes & Scheffer, 2004; Jackson, 2006). We agree with the view that plant taxa respond individualistically to environmental and climatic change (Bush, 2002), but we observe that many plant taxa do respond in concert, thus allowing recognition of altitudinally constrained vegetation zones that, indeed,

may change floristic composition over time (Hooghiemstra et al., 2012). Such change is well illustrated in the Holocene pollen records of La Cocha (González-Carranza et al., 2012) and Llano Grande (Velásquez–Ruiz & Hooghiemstra, 2013).

The use of discrete biome boundaries in this study is considered useful because of the scale sensitivity of the definition of boundaries. Small-scale analysis restrains the identification of zones of transition between biomes, while at a larger scale, such as along local transects, limits of vegetation belts are normally diffuse. However, in the latter case, discrete changes can occur where there are sudden shifts in abiotic conditions (Bach & Gradstein, 2011). For the scale of our analysis, and for the purpose of mapping changes in distribution and connectivity, biomes are first of all assessed as delimited vegetation associations (marked boundaries with limited transitions) along the altitudinal gradient. Subsequently, we discuss the implications of biome connectivity in the area of Lake La Cocha for the distributions of taxa based on current elevational occurrences. Hence, without disregarding the ongoing discussion on response mechanisms of plant associations to climate change (Feeley et al., 2011), we discuss connectivity implications for both levels of ecological responses to climate change, i.e., biome and species ecological responses.

METHODS

The pollen-driven connectivity framework was developed as follows: We summarized the main patterns of altitudinal biome distribution based on the La Cocha pollen record. We recognized four key distributions since the LGM. We characterized the landscape of the study area by its surface and relief variability along the elevation gradient. We then calculated the changes in surface of the different biomes as a two-dimensional (2-D), flat surface to compare surface estimates when taking into account the three-dimensional (3-D) relief. We estimated the degree of connectivity and surface loss of the páramo biome with an upslope-shifting UFL. Subsequently, we related rates of change in terms of spatial distribution of the different biomes to rates of change in terms of palynological taxa turnover, the latter reflecting the internal dynamics of forest. Finally, we discuss here the distribution patterns in relationship to the elevation ranges at both biome and species level.

BIOME DISTRIBUTIONS

We delimited an area of ca. 7600 km^2 around Lake La Cocha, defined to include the following four biome types: lowland forest, sub-Andean forest, Andean forest, and páramo. Permanent snow was included as a separate class. Here, we follow the altitudinal vegetation distribution as elaborated for the northern Andes by Van der Hammen (1974) and further specified for the southern Colombian Andes by Wille et al. (2001). The latter study provided estimates on the altitudinal compression of biomes and the variation in lapse rates between the relatively dry LGM setting and the more humid atmospheric conditions of the Holocene (Hooghiemstra & Van der Hammen, 2004). The temporal variability in altitudinal biome distribution was inferred from the La Cocha pollen record. The position of the UFL is characterized by a proportion of 40% arboreal pollen (AP%) (Hooghiemstra, 1984; Van't Veer & Hooghiemstra, 2000; Groot et al., 2011; González-Carranza et al., 2012). The AP%-based estimate of the UFL elevation is fine-tuned by considering the proportions of specific pollen and spore taxa with clearly constrained altitudinal ranges (Groot et al., 2013). The La Cocha pollen record shows that the UFL occurred around four main altitudinal positions during specific periods of time: (A) UFL located around 3550–3600 m (modern); (B) UFL around 2800 m (in the study area prevailing during the period of 8060–2860 cal yr BP); (C) UFL around 2400 m (in the study area prevailing during

the period of 14,085–8060 cal yr BP); (D) other pollen records (e.g., Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 1993; Van't Veer & Hooghiemstra, 2000) showed that the UFL was around 2000 m during the LGM at ca. 21,000 cal yr BP. The lowland forest biome, at present below ca. 1000 m elevation and during the LGM below ca. 800 m (Wille et al., 2001), is not reflected in the pollen spectra because heavy orographic rains prevent pollen grains from being transported from such low elevations to the lake.

SURFACE ESTIMATES OF THE BIOMES

In remote sensing studies, mapping ecosystem distribution at different time intervals is mostly based on the interpretation of satellite imagery of different years. Results are generally expressed as the area gained or lost by a certain type of land cover during the period of analysis. The resulting land cover maps do not take relief into account. This implies that the actual available surface area in montane regions is not fully explored. The most recent assessments of land cover change in the Andes overlooked landscape relief in surface estimates (Etter et al., 2006; Eva et al., 2012). To improve our understanding of connectivity dynamics, we integrated the relief into our surface estimates and the changing biome distributions. The 3-D landscape projection is considered both an approximation of available surface and dispersal distance. The surfaces are calculated in both 2-D and 3-D aspects (Fig. 1) with the Surface Volume tool of 3-D Analyst of ArcGIS, taking sea level as the horizontal reference plane (0 m.s.m.). Surface area estimates are analyzed for four biomes (lowland forest, sub-Andean forest, Andean forest, and páramo), and permanent snow is treated as a separate class for the four different UFL settings. Although palynological studies differentiate between subpáramo (3550–3800 m), grasspáramo (3800–4200 m), and superpáramo (4200 m to the permanent snow line) vegetation, we consider the páramo biome as a single unit in our spatial assessments. The method is further specified in Appendix 1. To model the UFL fluctuations and the corresponding biome surface areas we used a GIS-based algorithm developed by Rijsdijk et al. (2012, 2014). Originally designed to derive quantitative metrics from changing oceanic island sizes and configurations due to sea level fluctuations, we applied this method to assess "islands in the sky" by implementing an index for biome "islands" that are formed at high elevations. We use a digital elevation model (DEM) to calculate biome surfaces.

CONNECTIVITY

Landscape connectivity can be defined as the degree to which the landscape allows the migration of species (individuals) between the present habitats, facilitating gene flow. Two basic groups of connectivity can be considered: structural connectivity refers to the degree to which some landscape elements are contiguous or physically linked to one another (With & King, 1999; Tischendorf & Fahrig, 2000); functional connectivity recognizes the behavioral responses of organisms to the physical structure of the landscape (Taylor et al., 1993; Bélisle, 2005). Thus, landscape connectivity depends not only on the amount and patterning of habitat, but also on the habitat affinities and dispersal abilities of species (Laita et al., 2010). In our study we assess the effect of a shifting UFL on the structural connectivity of the restricted range distribution of the páramo. Due to the shifting of the boundaries between the biomes, their ranges shrink or expand significantly, resulting in a dynamically changing number of patches and their surfaces. Patches may merge or fragment, opening or closing dispersal routes within or between patches. The degree of connectivity and surface change depend on the relief, such as the presence of high peaks. Hence, the effect of the rise of the UFL on páramo connectivity can be more or less profound, depending on the landscape relief.

We used the probability of connectivity (PC) index developed by Saura and Pascual-Hortal (2007), which is based on network graph structures, the habitat availability, and interpatch dispersal probabilities. A graph structure evaluates the network as a set of nodes (patches) and links (corridors) such that each link forms the connection between two nodes. The distance between nodes (interpatch distance) is considered the dispersal distance for species (Pascual-Hortal & Saura, 2006) and is commonly used as the probability of dispersal within a network (Saura & Pascual-Hortal, 2007). The integration of intrapatch and interpatch connectivity with patch area into a single index has been shown to produce improved connectivity measurements compared to other indexes (Saura & Pascual-Hortal, 2007). To overcome limitations due to study area size (when the habitat patches are small compared to the total area), Saura et al. (2011) suggested the equivalent connected area (ECA) as the alternative index directly derived from the PC. The ECA is defined as the size of a single habitat patch (maximally connected) that would provide the same value of the probability of connectivity as the actual habitat pattern in the landscape. The equations used are further specified in Appendix 2. The computations of the PC and ECA index have been implemented in the Conefor Sensnode 2.2 software (Saura & Torné, 2009).

We calculated the overall network connectivity for the páramo biome along the elevation gradient as the UFL moves upslope from 2000 to 4100 m (currently at 3550 m). The páramo biome includes the sparsely vegetated superpáramo, currently occurring between 4200 m and the snowline. The patch connections were estimated using Euclidean (straight line) edge-to-edge distances between patches. Patches were considered as of equal habitat quality, and colonization is equally likely to occur from each patch. Fragmentation of the landscape (e.g., introduction of 200-m distances) initially has a greater effect on plants with poor dispersal capacity, while for plants with good dispersal capacity only increments of kilometers in distance will matter. For this reason, we included model outcomes with varying dispersal distances between 0.2 and 50 km.

RATES OF GEOGRAPHICAL AND PALYNOLOGICAL CHANGE

Based on the surface and connectivity estimates, three different geographical rates of change are obtained. The rate of elevation change (RoElev) of the UFL is calculated as the dissimilarity between reconstructed UFL positions in two adjacent pollen spectra, divided by the time interval between the spectra. The rate of surface change (RoSC) is obtained by calculating the dissimilarity between surface estimates in a 100-m elevation shift and at different altitudinal positions of the UFL. Additionally, changes in surface of the largest connected páramo patch (cp) are monitored along the altitudinal gradient. The rate of surface loss ($RoSL_{cp}$) is estimated for each 100-m elevation interval. High rates are considered indicative of where the patch undergoes a disconnection from an adjacent patch. Loss of connection is considered to occur when the patches are more than 1 km apart.

Estimates of changes in the species composition along environmental and climatic gradients provide information on the relationship between landscape features and the spatial patterns of biodiversity. Based on the pollen record of Lake La Cocha, rates of ecological change (RoEC) are estimated by calculating the palynological turnover rate (PTR) and the dissimilarity coefficient (DC) between adjacent pollen spectra. The PTR is defined here as the amount of taxonomic composition change per time unit. Pollen data were interpolated to produce intervals between samples equidistant in time. To account for the nonequivalent time intervals the DC is calculated as well. This coefficient is calculated as the distance between two samples in an N-dimensional space, with the coordinates defined by the pollen percentages of the pollen taxa in these samples (N

taxa) (Bennett & Humphry, 1995). Further explanation on rates of change implications is found in Appendix 3.

ALTITUDINAL DISTRIBUTION PATTERNS OF SPECIES

For pollen taxa well represented in the La Cocha pollen record, we downloaded all available herbarium records through the Global Biodiversity Information Facility (GBIF, 2013; Appendix 4). We followed the data filter method proposed by Feeley and Silman (2010) to reduce the potential influence of georeferencing errors and biased duplication of samples on the genus elevation distribution. This method includes screening the data to eliminate obvious georeferencing errors and duplicated records, resulting in a database of more than 67,000 unique records. We selected the records from Colombia and Ecuador as the most representative of the study area. For 49 genera represented by > 30 Global Biodiversity Information Facility (GBIF) records (collections), we estimated their altitudinal distributions. We only used elevation data recorded by the collections themselves, as elevations extracted on the basis of geographic coordinates are shown to present severe and problematic errors, especially in mountainous areas (Feeley & Silman, 2010).

RESULTS

BIOME AND UPPER FOREST LINE DISTRIBUTION IN THE LANDSCAPE

The landscape within the study area has been covered by a variety of spatial distribution patterns of the biomes through time (Fig. 2). The lake was surrounded by páramo up to 8060 cal yr BP (Fig. 2C, D), then by Andean forest after 8060 cal yr BP. During the LGM the large extension of permanent snow and páramo is evident, as is the fragmentation of the páramo into isolated patches at present time (Fig. 2A). These shifts of biomes along the slopes cause changes in surface area that show important differences between the biomes at these four different periods (Fig. 3). Andean forest shows a relevant increase in surface from 17% during the LGM to 57% at present (Table 2). Sub-Andean forest increased with similar values but a higher factor (5 compared to 3.2 for Andean forest). During the LGM permanent snow covered more than 20% of the study area and is absent today. Páramo covered 47% of the study area during the LGM; this area was reduced to 2% over the last 8000 years. The páramo vegetation occurs within an altitudinal range of 600 m (3600–4200 m), but nonetheless this biome covers only 2% of the area today. The largest gains occurred for Andean forest and sub-Andean forest (1622 km^2 and 1268 km^2, respectively) during the period that the UFL shifted upslope from 2800 to 3600 m, while during the same period of time the páramo lost 95% of its surface. Also during that period, the area with permanent snow lost 24 km^2, disappearing completely, while all forest biomes gained area.

CONNECTIVITY AND SURFACE

By projecting the reconstructed biome distributions to a more realistic 3-D model of the landscape (Fig. 1), approximations of variation in surface and distance can be better assessed. There are important differences in estimated surfaces as a flat area (2-D) versus as a 3-D projection (Table 3), especially in the mid-range altitudes between 900 and 2400 m. The total surface of the study area is 7559 km^2 as a 2-D flat surface but increases by 12% to 8467 km^2 when considered as a 3-D landscape. Surface estimates for the sub-Andean and Andean forest differ up to 15%–17%. The degree to which the 3-D model differs from a flat surface depends on the relief variability along the elevation gradient (Fig. 4A). The mountains around Lake La Cocha are characterized by abundant mid-range altitudes (2600–3400 m), with a steep reduction of available surface area in the adjacent higher and lower altitudes. The peaks in the 3-D/2-D line (Fig. 4A) point out where the relief deviates most from a flat surface, indicating

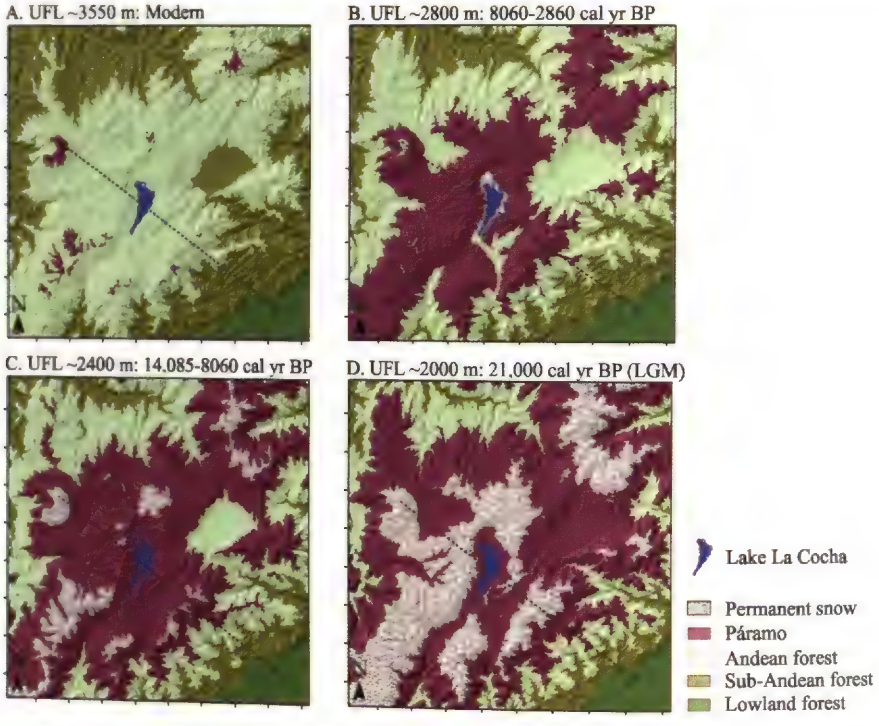

FIGURE 2. Distribution of lowland forest, sub-Andean forest (lower montane forest), Andean forest (upper montane forest), páramo (including subpáramo, grasspáramo, and superpáramo), and permanent snow during four different altitudinal positions of the upper forest line (UFL). —A. UFL at 3550 m, reflecting the present-day condition. —B. UFL at 2800 m, reflecting the period from 8060 to 2860 cal yr BP. —C. UFL at 2400 m, reflecting the period from 14,085 to 8060 cal yr BP. —D. UFL at 2000 m, reflecting the Last Glacial Maximum (LGM) at ca. 21,000 cal yr BP. The black lines indicate the direction of the altitudinal profile shown as the background of Figure 7.

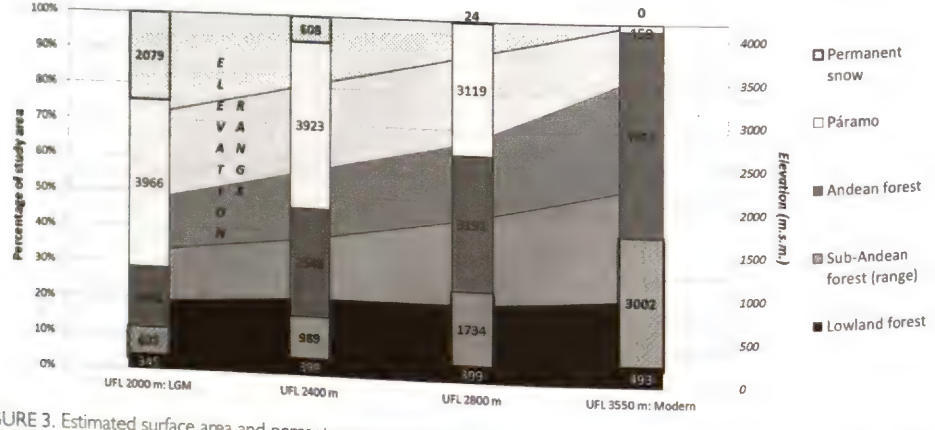

FIGURE 3. Estimated surface area and percentage cover of the four main vegetation associations and permanent snow for the following scenarios: upper forest line (UFL) located at 2000 m, 2400 m, 2800 m, and 3550 m elevation. The numbers within the bars indicate surface estimates (3-D, km^2) of the biomes. The total area of the study site is 7600 km^2. The elevation ranges of the biomes along the elevation gradient are shown in the background (right vertical axis). The altitudinal intervals occupied by the various biomes during periods of the last 14,000 years follow the La Cocha pollen record as specified in Table 2.

TABLE 2. Calculated change in surface area (2-D and 3-D) of main biomes and permanent snow for different upper forest line positions. Maximum values are indicated in bold.

	Elevation range (m)	Vertical extent (m)	Surface area in 2-D (km^2)	Surface area in 3-D (km^2)	Difference 3-D/2-D	Surface area 3-D
UFL ~3550 m: Period A (Modern)						
Permanent snow	0	0	0	0		0
Páramo	3600–4200	600	146	159	9%	2%
Andean forest	2300–3600	1300	4357	4813	10%	57%
Sub-Andean forest	1000–2300	1300	2589	3002	16%	35%
Lowland forest	< 1000	1000	467	493	6%	6%
UFL ~2800 m: Period B						
Permanent snow	> 3800	600	22	24	9%	0%
Páramo	2800–3800	1000	2892	3119	8%	37%
Andean forest	1900–2800	900	2768	3191	15%	38%
Sub-Andean forest	900–1900	1000	1492	1734	16%	20%
Lowland forest	< 900	900	385	399	4%	5%
UFL ~2400 m: Period C						
Permanent snow	> 3400	900	563	608	8%	7%
Páramo	2400–3400	1000	3567	3923	10%	46%
Andean forest	1600–2400	800	2192	2548	16%	30%
Sub-Andean forest	900–1600	700	852	989	16%	12%
Lowland forest	< 900	900	385	399	4%	5%
UFL ~2000 m: Period D (LGM)						
Permanent snow	> 3000	1300	1919	2079	8%	25%
Páramo	2000–3000	1000	3524	3966	13%	47%
Andean forest	1400–2000	600	1236	1442	17%	17%
Sub-Andean forest	800–1400	600	549	635	16%	7%
Lowland forest	< 800	800	331	345	4%	4%
TOTAL	**325–4200**	**3875**	**7559**	**8467**	**12%**	

steeper slopes at lower altitudes between 1000 and 2000 m. A similar variable landscape geomorphology is found between 2000 and 2700 m, indicating an increase in surface and dispersal distance. There are several more plane intervals between 2800 and 3400 m, with steeper slopes gradually increasing to higher elevations. This means that biomes with a distribution restricted to 2700 m and higher constitute an important part of the available surface area in the region. Nevertheless, each 100-m altitudinal rise results in a substantial reduction of the surface area and connectivity (Fig. 4B). The size of the largest connected páramo patch shrinks when its lower altitudinal boundary rises. At certain elevations, patches disconnect and dispersal routes between patches are lost. The first important decrease in connected surface occurs between 2700 and 2800 m, pointing to a first disconnection of a large area from the main patch. The result of this disconnection between the large páramo area in the northeast from the main páramo area surrounding the lake can be observed in Figure 2B. The next critical thresholds for connectivity loss occur between 3100 and 3300 m, and between 3400 and 3600 m (Fig. 4B). There, the topographical variation influences patch size and range shape of biomes. At the most profound fragmen-

TABLE 3. Calculated change in surface areas of main biomes and permanent snow as a 3-D landscape during the intervals between the four periods of characteristic UFL positions (Fig. 2A–D). Negative numbers indicate a decrease in surface area.

	Biome	Area change 3-D (km^2)	Change (%)
UFL 2800 to 3550 m.s.m. *Period B to A (Modern)*	Permanent snow	–24	–100
	Páramo	–2960	–95
	Andean forest	1622	51
	Sub-Andean forest	1268	73
	Lowland forest	94	24
UFL 2400 to 2800 m.s.m. *Period C to B*	Permanent snow	–584	–96
	Páramo	–804	–20
	Andean forest	643	25
	Sub-Andean forest	745	75
	Lowland forest	0	0
UFL 2000 to 2400 m.s.m. *Period D (LGM) to C*	Permanent snow	–1471	–71
	Páramo	–43	–1
	Andean forest	1106	77
	Sub-Andean forest	354	56
	Lowland forest	54	16

tation events, the rate of surface loss can decrease 40%–69%. Depending on the elevation interval, there is relatively more connectivity loss than surface area loss; each 100-m rise between 2000 and 3300 m affects the interpatch connectivity more than the intrapatch connectivity (Fig. 4C). As the lower páramo boundary further rises, more páramo patches disconnect, and intrapatch connectivity becomes more important. The degree of loss of the ECA also depends on potential dispersal distances, because initially species with a capacity for short-distance dispersal would experience higher ECA loss, while at higher elevations long-distance dispersal species become more affected.

GEOGRAPHICAL AND ECOLOGICAL RATES OF CHANGE

Geographical changes. The main pollen diagram of La Cocha (Fig. 5A) shows contributions of páramo, subpáramo, and Andean forest. The record of UFL positions (Fig. 5B) shows a high variability of RoElev at a short time scale (Fig. 5C), indicating average migration velocities up to 20 vertical m yr^{-1}. Some peak values of upslope UFL shifts are based on single pollen samples and are considered meaningless outliers (indicated with asterisks in Fig. 5B). As the forest moves upslope a larger surface extension is occupied in the region (Fig. 5D). Both Andean and sub-Andean forests expand, while páramo, in particular, is replaced by Andean forest (Fig. 5D).

Shifts of the UFL show several peaks (Fig. 5B) toward higher altitudes, causing sharp decreases in the representation of the subpáramo biome (Fig. 5A). During the period from 13,000 to 11,500 cal yr BP (Fig. 5A, zones 3 to 4) subpáramo nearly disappeared (González-Carranza et al., 2012). Significant peaks are also present between 8000 and 1000 cal yr BP; human presence is evidenced in the Andes during this period, yet we consider this part of the record to be reliable. However, during the last 1500 years (Fig. 5,

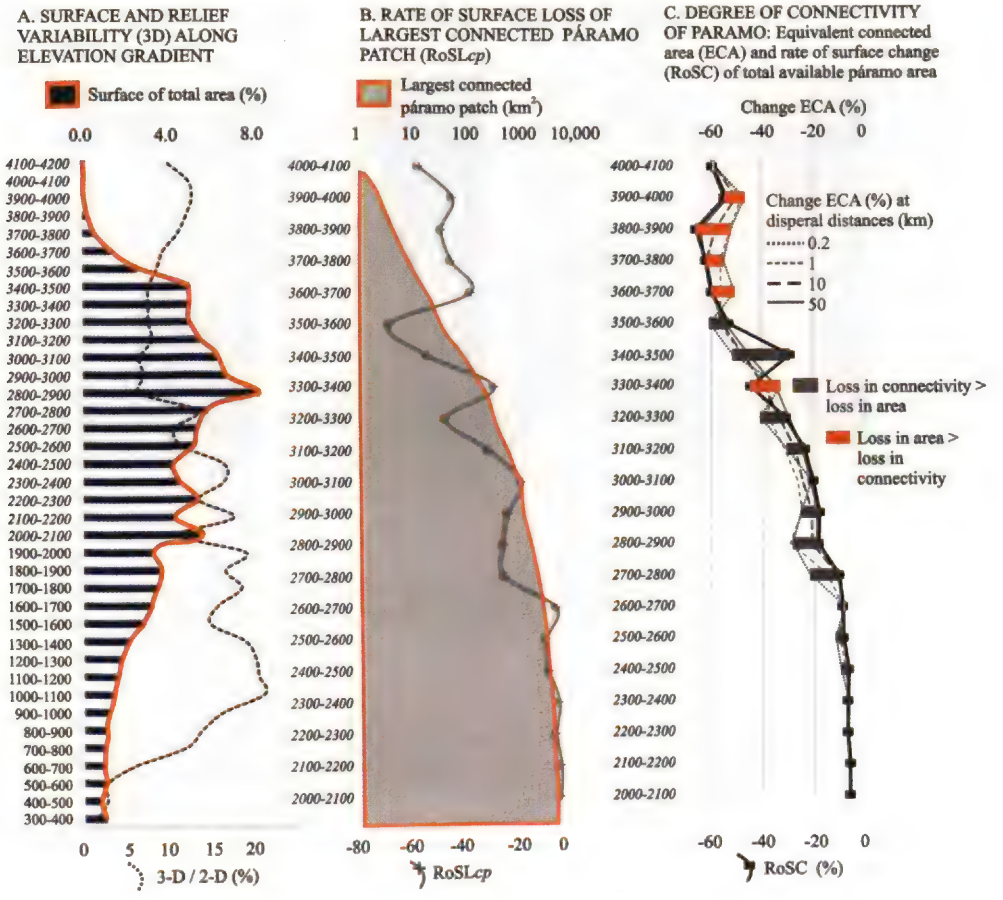

FIGURE 4. —A. Surface and relief variability along the elevation gradient expressed as the percentage cover as a function of the selected study area and the 3-D/2-D ratio (%). —B. Surface (2-D, km^2) and upslope rate of surface loss of the largest connected páramo patch area (RoSL*cp*, %). Surface area is along a logarithmic scale and patch surface is estimated in absence of permanent snow. —C. Changes in equivalent connected area (ECA) along the elevation gradient as the indicator of páramo connectivity. The ECA values for varying dispersal distances (0.2–50 km) are plotted as lines, as is the rate of total surface area change (RoSC, %). Orange bars indicate where loss in area is larger than the relative loss in connectivity. Dark gray bars indicate where loss in connectivity is larger than the relative loss in area.

zones 20 to 23) there was significant anthropogenic impact (deforestation), and the record for this period was discarded as invalid. Periods in which the UFL reached high elevations (3100–3300 m) may not always show a profound effect on the total biome surface area (Fig. 5D), but they record a heavily reduced extension of the largest páramo patch (Fig. 5E), indicating reduced connectivity (Fig. 4).

The critical elevation limits for páramo patches to disconnect depend on the lowest elevation thresholds in the landscape and the elevation of the summits. When the UFL moves upslope, the number of patches increases and the distribution is increasingly confined to a group of patches (Fig. 6: C3) or isolated peaks (Fig. 6: C1, C2, C4, C5) in the landscape. For the region of La Cocha the first critical elevation trespass is between 3100

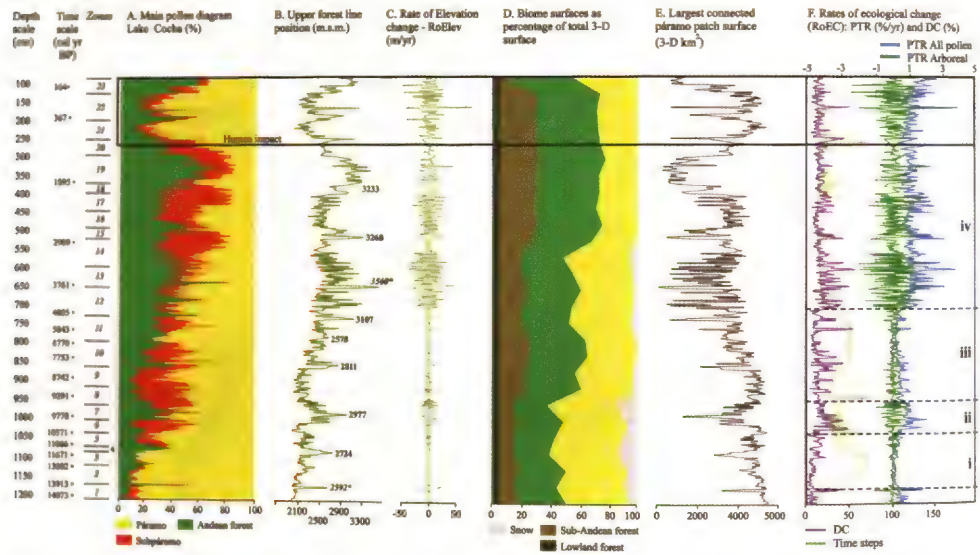

FIGURE 5. Records of vegetation dynamics and rates of change. The left vertical axis indicates, from left to right, the depth scale, time scale, and pollen zones. —A. Main pollen diagram of core La Cocha-1 (after González-Carranza et al., 2012). —B. Upper forest line (UFL) position. The elevation peaks are indicated where the rapid increase of the UFL caused the disappearance of the subpáramo. Values with * are based on a single sample and therefore discarded. —C. Rate of elevation change (RoElev, m yr^{-1}). —D. Biome surface areas of four vegetation associations and permanent snow as percentage of total 3-D surface. —E. Area (3-D, km^2) of largest páramo patch surface. —F. Rates of ecological change (RoEC): palynological turnover (PTR, %/yr) for the total and arboreal pollen sum, and dissimilarity coefficient (DC, %). Time steps of the age model are shown along the lower horizontal axes. Horizontal dashed lines indicate transitions between periods of higher (ii and iv) and lower (i and iii) species composition dynamics.

and 3200 m, when C1 disconnects from C6 and consequently, from the rest of the landscape. C2 disconnects at 3300 m, while important stepping stone patches previously present between C1 and C6 also disappear. These changes are more prominently affecting connectivity as seen in Figure 4. When the UFL moves further up to 3400 m, C6 practically disappears and loss in area is substantial in all components. C5 now becomes a group of separated patches. Connectivity is greatly affected when C3 disintegrates and C2 is nearly lost; this happens when the lower boundary migrates to 3600 m. Up to that limit páramo occurs relatively close to the lake on the surrounding ridges. Considering projections of a future upslope shift of the UFL, the páramo biome will only remain on the Galeras volcano (C1) as a last refugium (but the volcano has had several eruptions in the last two decades, potentially damaging the vegetation in the refugium).

Ecological changes. Transitions between periods of increased PTR (Fig. 5F: ii, iv) and decreased PTR (Fig. 5F: i, iii) are observed for both general and arboreal pollen composition. Intervals of increased PTR possibly indicate periods of variable climate conditions. The length of the time steps between pollen samples varies along the core from 20 to 70 years (Fig. 5, time step curve). The most striking observation to emerge from the PTR and time step comparison is the clear relation between PTR and the length of the time steps; long time steps weaken PTR dynamics. The DC also shows the same transitions between periods of increased and decreased variability, but to a lesser degree (Fig. 5F). Comparing the UFL position with the

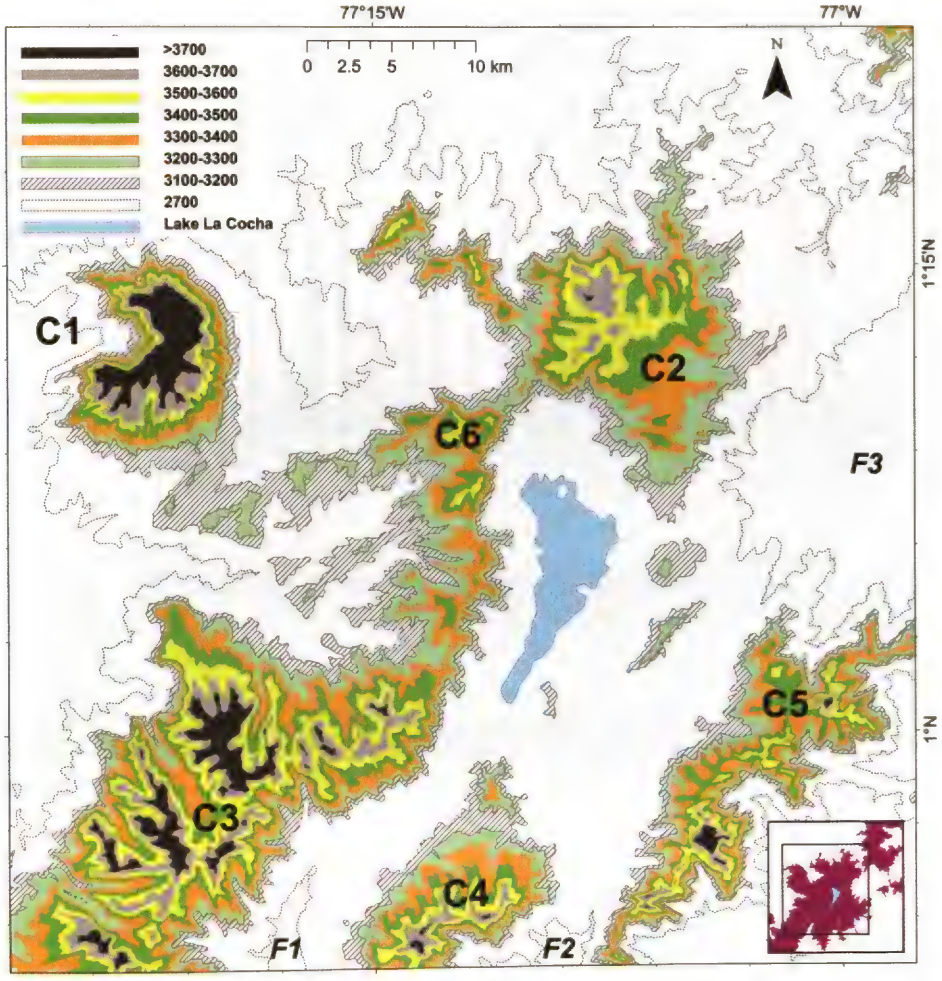

FIGURE 6. Geographical representation of the critical elevation thresholds of páramo connectivity and surface changes (Fig. 4) in a selected area in the region of Lake La Cocha. The small window in the lower right corner delimits the location of the selected area from within Figure 2B, showing the páramo extension. Shaded areas indicate elevation ranges of 100-m intervals (see legend), and the dashed line delimits the 2700-m elevation contour. Components (C) indicate groups of páramo patches. Forest areas toward lower elevations (< 2700 m) are indicated as F1, F2, and F3, the last one being the Basin of Sibundoy (Fig. 1).

DC values, there is tendency of increased DC when forest occurs at higher elevations (> 2600 m; Fig. 5B). Interestingly, the higher elevations are related to increased surface extensions (Fig. 5D), which indirectly point to a relationship between extended range of biomes and the DC.

The distribution of individual species along an elevation gradient is composed of a nucleus zone, which represents the core of the species' range plus the trailing and leading edges of biogeographical boundaries of the species' distribution. Shifts in the geographic ranges of individual plant species, as well as whole plant associations, occur by expansion of the population at the leading edge of the distribution area and retraction at the trailing edge (Jump et al., 2009). Species may show a re-

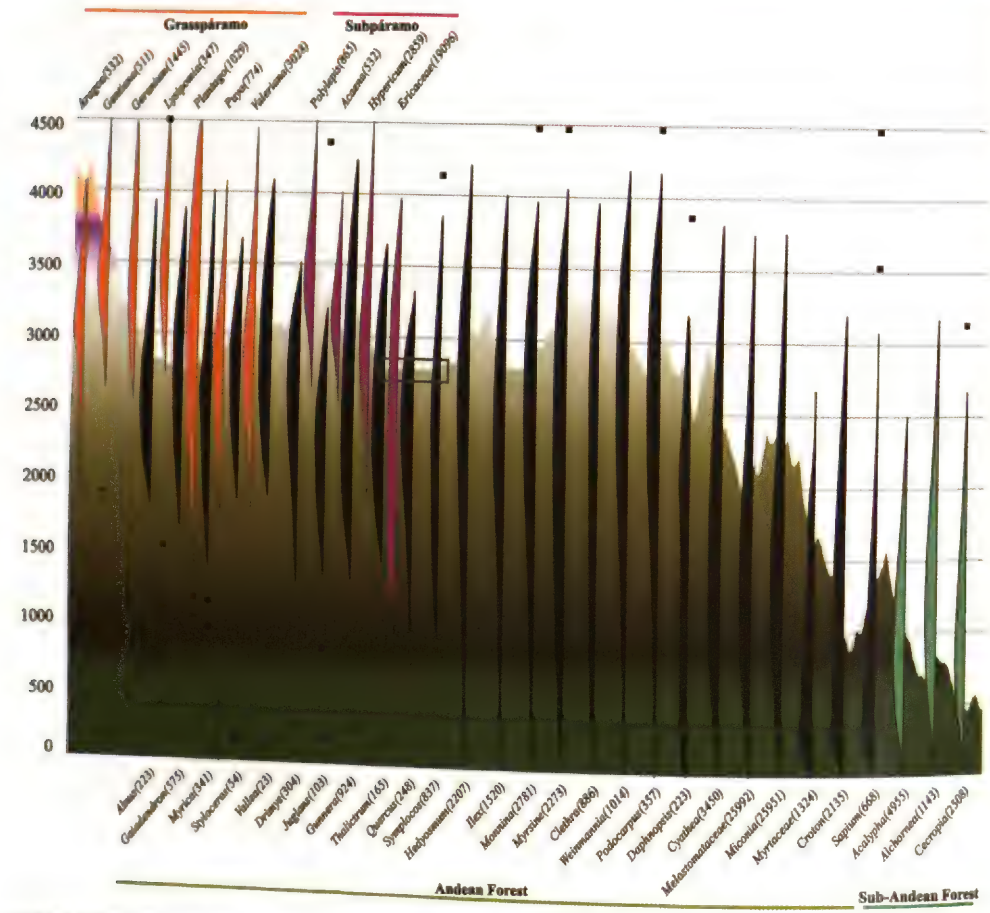

FIGURE 7. Altitudinal ranges of modern plant species present in pollen records from the northern Andes. The sequence of taxa follows the grouping of pollen taxa reflecting specific biomes. The curves follow the shape of the frequency distributions: the thickest part of the curve indicates the highest frequencies of the observed distribution. Outliers are indicated as dots. The number of herbarium collections included per taxon is specified in parentheses. The background shows the landscape profile of the region as drawn in Figure 1. The location of Lake La Cocha is indicated by a box. Distribution data were obtained from the Global Biodiversity Information Facility (GBIF, 2013).

stricted nucleus range, while others show a relatively broad core range and distribution along a wide elevation gradient (Fig. 7). Several arboreal genera are distributed over the entire range of altitude, such as *Podocarpus* L'Hér. ex Pers., *Weinmannia* L., and *Hedyosmum* Sw. The trailing and leading edges of species distributions are relatively widely spread along the elevation gradient, for both high montane as well as for lowland species. The distribution of subpáramo species does not differ from the grasspáramo species; both the nuclei and edges show similar patterns. This justifies the strategy chosen for this analysis, to assess páramo dynamics as a single biome. The leading edges of the Andean forest biome overlap the core ranges of the páramo biome, although the nuclei of the arboreal species are all below 3000 m. This reflects the difference between all GBIF-loaded data from Colombia and Ecuador leading to an average position of the UFL ecotone, and the region-

specific positions of the UFL ecotone as used in the various pollen studies: UFL in Llano Grande at 3450 m (Velásquez-Ruiz & Hooghiemstra, 2013); in Fúquene at 3200 m (Groot et al., 2011, 2013); in La Cocha at 3550 m (González-Carranza et al., 2012); and in Guandera at 3600 m (Bakker et al., 2008). Depending on MAT, MAP, cloudiness, and night frost (Hooghiemstra et al., 2012), the altitudinal ranges of some species can differ significantly between the forest and páramo biomes, while many others occur in the mid-ranges.

DISCUSSION

GEOGRAPHICAL AND ECOLOGICAL CHANGES

Spatial analysis of the landscape provides the geographical context to better understand climate-driven biome dynamics. The ratio between the elevation range and the associated available biome surface area depends on the relief only. In the study area, biomes at mid-range altitudes have higher surface area available compared to biomes prevailing at high and low altitudinal ranges (Fig. 4). Although biomes may not show substantial surface change along the elevation gradient, certain 100-m shifts have profound effects on their connectivity. The degree of fragmentation depends on the altitudinal range. The projected loss of biome surface due to global warming is disproportionately large compared to the reduction in elevation range which is typical of a mountain setting (Bush, 2002). As a consequence, the most important surface reductions are processes of isolation between patches of biomes.

Fast UFL shifts, indicative of rapid climate change, cause critical consequences for the connectivity of the páramo biome (Fig. 5). Trees with pioneer qualities and a short life cycle allow a fast response to climate change and may expand into new areas and produce fertile individuals within less than two decades. A high variability in UFL positions at short time scales indicates average migration velocities up to ca. 20 vertical m yr^{-1}, with peaks up to 40 vertical m yr^{-1}. Estimates of migration in deep ecological time based on fossil pollen records are known to be significantly higher than observed rates from dispersal studies based on plots in the field (Pearson & Dawson, 2005). Estimates based on fossil records from temperate lakes mention rates of horizontal spread exceeding 1000 m yr^{-1} (Davis, 1981; Huntley & Birks, 1983), but these velocities have not been observed from ecological studies (Clark, 1998). Ecologists suggest that rare long-distance dispersal of pollen grains may explain the higher migration rates inferred from pollen records (Clark et al., 2001; Pearson & Dawson, 2005; Nathan, 2006). This is substantiated by Jansen et al. (2013), who showed in a case study from northern Ecuador that when grass-rich biomes prevail, their pollen signal may lead real forest change by about a thousand years. Willis et al. (2010) argued that although the underlying mechanisms responsible for past changes in climate were very different, the rates and magnitude of climate change were similar to those predicted for the future and therefore relevant to understanding future biotic response. What emerges from records of deep ecological time is evidence for rapid community turnover, migrations, development of novel ecosystems, and thresholds from one stable ecosystem to another. In Figure 5B, the arboreal pollen peaks based on single pollen samples and peaks that start to grow from below 40% (Fig. 5A) (thus reflecting páramo conditions at the coring site) are considered unreliable (i.e., peaks labeled 2592* and 3560*).

Patches of forest within the páramo are thought to contribute to fast expansions when conditions become favorable (Ammann et al., 2000; Bush, 2002; Sarmiento & Frolich, 2002; Pearson, 2006). When the UFL passes the level of the lake at 2800 m the surrounding ridges still host páramo vegetation at a very close distance. Even at the highest peak of the UFL at 3268 m (Fig. 5B), páramo is still present directly around the lake. This makes a local extirpation of the subpáramo as an ecotone plausible when the leading edge of

forest is overpassing the slower-migrating lower edge of the subpáramo biome (Breshears et al., 2008).

Replacement of forest by páramo vegetation is considered a slower process. When climate conditions become unfavorable for trees in the current ecotone, individual trees may die, leaving abundant dead wood prone to fire. After opening the landscape by fire, subpáramo is able to become reestablished as a transition zone between grasspáramo and the retreating forest. A lag greater than 100 years between the climate deterioration and the downslope retraction of the forest seems feasible. The pollen record of La Cocha indeed shows horizons with abundant charcoal at events of forest retraction (González-Carranza et al., 2012). Rapid ecosystem reconfigurations between alternative states are known as ecological regime shifts (Andersen et al., 2008; De Boer et al., 2013). The trigger may be an external perturbation, such as climatic fluctuations, or a change in the system's internal dynamics. The longest period of relative stability is 600 years at Lake La Cocha, while a period of 400–1500 years was observed at Lake Fúquene (Bogotá-Angel et al., 2011).

Mountain slopes between ca. 1000 and ca. 1500 m were permanently covered by the Andean forest, following the hypothesis of Wille et al. (2001) that this particular interval is unique because the biome cover has remained unchanged since the LGM. This implies that pollen records from the ca. 1000–1500 m interval are less sensitive to minor climate change. Although the PTR is proposed as a useful indicator for the speed of past vegetation change (Jacobsen et al., 1987; Williams et al., 2001; Urrego et al., 2009), care should be taken in extracting easy conclusions from the RoEC estimates, since variation in time intervals has significant impact. In the La Cocha pollen record, temporal steps vary between 5 and 70 years, respectively enforcing and weakening the PTR values. Without the corresponding data on time step variability and absolute pollen change values, rates of change estimates could lead to misinterpretation of the degree of biome change. Therefore, we suggest standardizing the notion of time step variability for PTR and RoEC estimates as a common denominator in future studies.

NO-ANALOGUE VEGETATION COMPOSITION

The most dynamic altitudinal range for species in the region of Lake La Cocha is between 2500 and 3500 m. Here several biological and geographical processes converge: the characteristic geomorphology of the region (Fig. 4); the isolated habitat patches at distinct elevation levels (Fig. 6); and the distribution nuclei of species within this range (Fig. 7). At the same time this is an important elevation range for surface availability (Fig. 4). The relief plays an important role in species sorting and their potential versus realized distribution. The species with greatest amplitude, arboreal species in this study, are distributed over the entire range of altitude (Fig. 7). This offers opportunities for rapid expansion when conditions improve toward higher altitudes or from isolated patches that remained in the landscape. Altitudinal range width of ecosystems and species influence the observed patterns of species richness and the homogeneity along the elevation gradient (Bach et al., 2007). The tendency to observe higher turnover rate at mid- and higher elevations is explained by the convergence of upper and lower elevation distribution limits and the density of distribution nuclei of the different biomes along this elevation range (Bach et al., 2007). Nevertheless, the UFL and the transitions from the foothills to the flat lowland terrain are well-known zonations (Kessler, 2000; Richter et al., 2008).

FUTURE IMPLICATIONS

The timing, magnitude, and direction of biotic responses to projected future climate change is thought to vary greatly among species and geographical conditions, allowing novel plant assemblages as well as different types of distribution

patterns to develop (Williams & Jackson, 2007; Breshears et al., 2008; Willis et al., 2010; Chen et al., 2011). Since the last interglacial period, biotic communities have been resorted, leading to the formation of new species assemblages linked to new climatic conditions (Jackson & Williams, 2004; Willis et al., 2010; Bertrand et al., 2011). Assuming that Andean montane species distributions are significantly influenced by temperature (as well as precipitation, atmospheric pCO_2, clouds, night frost frequency, and UV radiation; Hooghiemstra et al., 2012), the projected future climate warming (IPCC, 2007) will probably cause an upward migration of species in montane arboreal communities, since temperature decreases predictably with increasing elevation. The effect on páramo connectivity and available habitat area is projected to be substantial (Fig. 4). Currently, the pressure on ecosystems has reached a dangerous level due to the combination of rapid climate change and extended land use (Travis, 2003). The greatly reduced range sizes of natural systems due to grazing and other activities can pose barriers for upslope shifts of the leading edges of forests, if the surrounding forests and natural habitats are not maintained (Chen et al., 2009). The key is to understand the ecological network across elevation gradients and, thus, the reason to focus local conservation efforts on guaranteeing habitat availability and connectivity in the montane landscape. The improved insight on the ecological complexities obtained through the framework developed in this paper should be applicable to studies in a wide range of disciplines, such as evolutionary and genetic studies, biogeography, landscape ecology, and landscape conservation.

CONCLUSIONS

Some exciting insights were developed by assessing palynological reconstructions in a landscape perspective. Biome and species distribution patterns, their responses to climate change, and critical landscape thresholds for connectivity in montane areas have been integrated. The assessments concerning connectivity directly inform our understanding of montane biome dynamics through time and space. The applicability of this innovative approach is shown for the pollen record of Lake La Cocha. The region offers a very diverse migratory environment as available habitat surface, dispersal distances, and connectivity differ along the elevation gradient. These characteristic landscape features clarify the observed differences between the biomes in terms of rates of surface, and altitudinal, and palynological change. We showed that care must be taken in the interpretation of palynological change as an indicator of dynamics, because trends are related to the lengths of the time steps in the record. Since the LGM, forest biomes have increased while páramo is being pushed to a narrower altitudinal range due to the rising UFL along the slope. These shifts of the UFL can be swift (20 vertical m yr^{-1} and more), causing the local extirpation of the ecotone biome (subpáramo) between páramo and forest and important losses in connectivity of páramo. Although the present-day páramo biome reflects only 4% of its LGM extension, its level of diversity seems untouched. During Pleistocene times the gene pools of these species must have passed such bottlenecks multiple times. This has interesting implications for future dynamics in gene pools; keeping connectivity available is a crucial prerequisite for long-term conservation of the gene pools.

The prime elevation zone where biological and geographical dynamics converge in the region of Lake La Cocha is between 2500 and 3600 m. Within this range, different biomes have dominated through time, there is a higher surface availability, and there are shorter dispersal distances compared to higher and lower elevations. Here, species from different biomes overlap in their potential distribution, and loss of interpatch and intrapatch connectivity of the páramo biome is most profound. Furthermore, when the forest expands to these higher elevations, there is a tendency

for diversification of species assemblages (as estimated by the PTR and DC), indicating the temporal overlapping of altitudinal distribution of biomes within the same altitudinal range. The concurring potential altitudinal ranges of species observed in current distribution records confirm that finding. Spatial assessments of the landscape need to be incorporated into palynological thinking to improve the interpretation of biome and species responses to climate change. The application of palynological research for conservation strategies is urged to expand its potential. Its integration with other disciplines will have far-reaching implications.

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APPENDIX 1. Three-dimensional calculations of surface in ArcGIS.

The landscape of a study area can be analyzed as if it were a flat 2-D area (Fig. 1; custom surface) or as a dynamic diverse feature (Fig. 1; floating on a custom surface), in this study showing the relief around Lake La Cocha. To estimate the available surface of the different biomes at different moments in time, the digital elevation model (DEM) (Jarvis et al., 2008) is projected from 2-D into a 3-D representation. Therefore, the DEM is converted into a so-called triangular irregular network (TIN), which is a continuous, non-overlapping triangular network representing the surface topography of an area. The boundaries of each triangle define the position of linear features that play an important role in a surface, such as ridgelines or stream course. Each corner of a triangle has a z-value, which is the value of the altitude. To create a TIN within ESRI ArcGIS 10 (Redlands, California, U.S.A.), a contour map of the available 90 m DEM is created with soft isolines between every 25 m, which is then converted into the final TIN. For surface modeling, TINs should be constructed using projected coordinate systems, as geographic coordinate systems are not recommended because their angular units of degrees can produce incorrect results in slope, volume, and area calculations. Consequently, the surface of the created TINs is calculated in both 2-D and 3-D aspects with the Surface Volume tool of 3-D Analyst of ArcGIS, taking sea level as the horizontal reference plane (0 m.s.m.). Surface area estimates are analyzed for all biomes during the four different UFL settings and also for the altitudinal range of the total study area.

APPENDIX 2. Connectivity index.

The connections between habitat patches are best characterized by a probabilistic model in which there is a certain probability of dispersal among patches typically modeled as a decreasing function of interpatch Euclidean or effective distance (Saura & Pascual-Hortal, 2007). These probabilities are defined as the chance that two species randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections (p_{ij}) between them. The probability of connectivity index (PC) is given by the following expression (Saura & Pascual-Hortal, 2007):

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p^*_{ij}}{A_L^2}$$

where ai and aj are the areas of the habitat patches i and j, and A_L is the total landscape area (area of the study region, comprising both habitat and non-habitat patches). PC increases with improved connectivity and has a bounded range of variation between 0 and 1. PC equals 0 when no habitat patches are present in the study area, and equals 1 when all the landscape is occupied by habitat. The strength of each link is characterized by pij, which is the probability of direct dispersal between patches i and j. The value for p*ij is the maximum product probability of all the possible links between patches i and j (including the direct patch between i and j).

It is calculated as follows:

$$ECA = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p^*_{ij}}$$

The equivalent connected area (ECA) value will not be smaller than the area of the largest patch in the landscape. The value of the ECA will coincide with the surface area of the single habitat patch (no fragmentation) or when the habitat is fragmented into different patches but there is a maximal interpatch connectivity such as that p*ij = 1 for each pair of patches (Saura et al., 2011).

APPENDIX 3. Rate of change estimates.

Greenland ice cores revealed the first hint at how fast climate can change. Based on $\partial^{18}O$ records, the Dye3 record showed a 7°C temperature increase in ~50 years (Dansgaard et al., 1989) and the North Greenland Ice Core Project (NGRIP) record documents 11.2°C in 21 years (Dahl-Jensen et al., 2002; NGRIP Members, 2004). Understanding of rates of change in terrestrial ecosystems is poorly developed, but first studies report results that have significant implications. Millennial-scale variability in precipitation was reported by Cruz et al. (2009) for Brazil and by Baker et al. (2009) for Peru. Vimeux (2009) studied similarities and discrepancies between records from tropical Andean ice cores and high-latitude ice sheets and discussed mechanisms to propagate drivers from high to low latitude. Urrego et al. (2009) studied rates of change (RoC) from 13 Neotropical pollen records and identified periods of fastest change since the Last Glacial Maximum (LGM). They state that RoC analysis showed that the speed of these climate changes never exceeded the species response capabilities. However, the RoC values were not specified nor directly compared to species response indicators. The robust age model of the new Fúquene-9Composite (Fq-9C) record (Groot et al., 2011) allowed inference of first estimates of RoC in the upper part of the montane forest in Colombia and showed that the fastest change of 10°C ± 2°C occurred at terminations and during marine isotope stage (MIS) 3. All this evidence is indicative of teleconnections between the high latitudes and Neotropical low latitudes, and Grimm and Ambrizzi (2009) and Khodri et al. (2009) discuss several mechanisms.

APPENDIX 4. Full reference for the GBIF Data Portal.

Global Biodiversity Information Facility—GBIF Data Portal. 2013. Biodiversity occurrence data published by: Administración de Parques Nacionales, Argentina; Arizona State University, Global Institute for Sustainability; Asociación de Becarios del Casanare—ABC; Australian National Herbarium (CANB); Berkeley Natural History Museums; Bernice Pauahi Bishop Museum; Biologiezentrum Linz Oberoesterreich; Bioversity International; Botanic Garden and Botanical Museum Berlin-Dahlem; Botanical Research Institute of Texas; British Antarctic Survey; California Academy of Sciences; Canadian Biodiversity Information Facility; Centro Nacional Patagonico—CONICET; Comisión nacional para el conocimiento y uso de la biodiversidad; Conservation International; Corantioquia; Facultad de Ciencias Naturales y Museo—U.N.L.P.; Fairchild Tropical Botanic Garden; Federación Nacional de Cafeteros de Colombia; Field Museum; Fundación Alma; Fundacion Miguel Lillo Provider; GBIF New Zealand; GBIF-Spain; GBIF-Sweden; Georg-August-Universität Göttingen, Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik; Harvard University Herbaria; Herbaria of the University and ETH Zürich (Z+ZT); Herbario SANT, Universidade de Santiago de Compostela; Herbarium Hamburgense; Herbarium of the University of Aarhus; Herbarium of Université de Montpellier 2, Institut de Botanique; iNaturalist.org; INRA Antilles-Guyane; Institute of Botany, University of Hohenheim; Instituto de Botánica Darwinion—CONICET; Instituto

de Ciencias Naturales; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Instituto Nacional de Biodiversidad (INBio), Costa Rica; Instituto Nacional de Tecnologia Agropecuaria—Instituto de Recursos Biológicos; Karl Franzens University of Graz, Insitute for Botany—Herbarium GZU; Ministerio de Ciencia, Tecnología e Innovación Productiva; Missouri Botanical Garden; MNHN—Museum national d'Histoire naturelle; Mountain Invasion Research Network—MIREN_ETH; Museo Argentino de Ciencias Naturales; Museo Nacional de Costa Rica; National Herbarium of New South Wales; National Museum of Natural History, Smithsonian Institution; National Museum of Nature and Science, Japan; Natural History Museum, Vienna—Herbarium W; Netherlands Centre for Biodiversity Naturalis, section National Herbarium of the Netherlands; Organization for Tropical Studies; Royal Botanic Garden Edinburgh; Royal Botanic Gardens, Kew; Royal Ontario Museum; Senckenberg; Staatliche Naturwissenschaftliche Sammlungen Bayerns; SysTax; the New York Botanical Garden; UNIBIO, IBUNAM; Universidad de La Salle; Université de Montréal Biodiversity Centre; University of Alabama Biodiversity and Systematics; University of Arizona Herbarium; University of British Columbia; University of California, Davis; University of Connecticut; University of Malaga; University of Vienna, Institute for Botany—Herbarium WU; US National Plant Germplasm System; Utah Valley State College (UVSC); Wrocław University, Museum of Natural History; Yale University Peabody Museum (accessed through data.gbif.org; 28 April 2013 and 4 May 2013).

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CHAPTER 7

FRUITS OF *OREOMUNNEA* (JUGLANDACEAE) IN THE EARLY MIOCENE OF PANAMA

Fabiany Herrera, Steven R. Manchester, Rebecca Koll, and Carlos Jaramillo*

ABSTRACT

Permineralized fruits of Juglandaceae have been recovered from the Early Miocene Cucaracha Formation exposed in excavations of the Panama Canal. Transverse sections and peels reveal that the nuts are subdivided into eight chambers at the base, and the nutshell and septa are composed mainly of fibers. Together, these features are found only in the Neotropical juglandaceous clade composed of extant *Alfaroa* Standl. and *Oreomunnea* Oerst. Based on the small nut size and relatively thin wall and septa, these nuts are assigned to *Oreomunnea*, which is distinguished from extant *Alfaroa* by its winged fruits adapted for wind dispersal. A. Graham first reported pollen grains of the *Alfaroa/Oreomunnea* type from the Miocene of Panama. The new fossil fruits of the Cucaracha Formation are the earliest macrofossil record of *Oreomunnea*, enhancing our understanding of the phytogeographic history of Juglandaceae in Central America. If this newly described fossil species, *O. grahamii* Manch. & Herrera, grew in similar ecological settings to those of its modern counterparts, the fossils may be an indicator of the medium-high paleotopographic relief of Panama during the Early Miocene.

Key words: Alfaroa, fossils, fruits, Juglandaceae, Miocene, *Oreomunnea*.

The Juglandaceae have an excellent fossil record in the Northern Hemisphere, well represented by pollen, leaves, wood, catkins, and fruits. This record includes most of the extant genera, plus a few extinct ones in the Paleogene (Manchester, 1987, 1989; Elliot et al., 2006). Some extinct upper Cretaceous genera based on flowers containing Normapolles pollen from Europe may belong on the stem lineage of Juglandaceae (Friis, 1983; Friis et al., 2006). However, the modern Neotropical genera *Alfaroa* Standl. and *Oreomunnea* Oerst. have mostly eluded detection in the macrofossil record.

Ten genera in two subfamilies are recognized for the Juglandaceae (Manos & Stone, 2001; Manos et al., 2007), although a broader circumscription of the family that includes *Rhoiptelea* Diels & Hand.-Mazz. (traditional Rhoipteleaceae) has gained some acceptance (APG, 2009). *Rhoiptelea* appears as sister to Engelhardioideae (*Alfaroa*,

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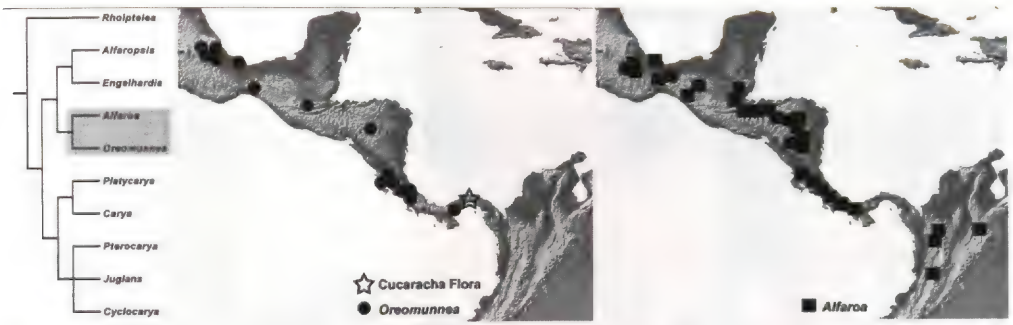

FIGURE 1. Left: phylogenetic relationships of genera in Juglandaceae (modified from Manos et al., 2007; Sauquet et al., 2012). Center: occurrence of extant *Oreomunnea* and location of Early Miocene Cucaracha flora. Right: occurrence of extant *Alfaroa* (data accessed through GBIF Data Portal, Global Biodiversity Information Facility, data.gbif.org, accessed 9 April 2013). Base maps courtesy of National Aeronautics and Space Administration Jet Propulsion Laboratory, California Institute of Technology.

Alfaropsis Iljinsk., *Engelhardia* Lesch. ex Blume, *Oreomunnea*) and Juglandoideae (*Carya* L., *Cyclocarya* Iljinsk., *Juglans* L., *Platycarya* Siebold & Zucc., *Pterocarya* Kunth) (Manos et al., 2007; Sauquet et al., 2012). There are about 60 species, distributed mainly in the Northern Hemisphere of both the Old and New World, although some genera reach the Southern Hemisphere and tropical latitudes (Stone, 1989, 1993). *Oreomunnea* and *Alfaroa* are usually components of mountain forests. *Oreomunnea* is distributed from Mexico to Panama (Fig. 1), with two living species. It was formerly considered to be congeneric with the Asian genus *Engelhardia* (including *Alfaropsis*), because of similar winged nuts with a prominent trilobed wing developed from a persistent inflorescence bract (Fig. 2). However, Stone (1972) built a strong case for retaining generic status for *Oreomunnea*, noting in particular that its two species share more in common morphologically with *Alfaroa* than with *Engelhardia*. Distributed from southern Mexico to northern Colombia (Fig. 1), *Alfaroa* has five extant species (Stone, 2010). It has wingless fruits (Fig. 2), but retains an inconspicuous 3-lobed inflorescence bract at the base of the developed fruit. Subsequent molecular work (Manos & Stone, 2001; Manos et al., 2007; Sauquet et al., 2012) indicates that *Oreomunnea* and *Alfaroa* form a clade that is sister to the Asian clade composed of *Alfaropsis* (former *Engelhardia roxburghiana* Wall.) and *Engelhardia* (Fig. 1).

Although no macrofossils of *Oreomunnea* and *Alfaroa* had been identified yet in the Neotropics, Graham (1988b) noted the occurrence of triporate juglandaceous pollen, which he referred to as *Alfaroa/Engelhardia* from several sites in the Neogene of Panama, including the Early Miocene Cucaracha and La Boca formations (Graham, 1989), and the Eocene Gatuncillo Formation (Graham, 1985). He also reported *Alfaroa/Engelhardia* pollen grains from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and Haiti (Graham, 1990). With subsequent acceptance of extant *Oreomunnea* as a genus distinct from the Old World *Engelhardia*, Graham (1991) revised the identification of this pollen morphotype to *Alfaroa/Oreomunnea*, while noting that in the stratigraphic literature this pollen type is generally known as *Momipites*. Although some of the extant genera of Juglandaceae are readily distinguished from one another by features of pore number and distribution and patterns of exinous thickening and thinning, the four genera of subfamily Engelhardioideae are very similar in pollen morphology, each having triporate isopolar grains. With transmission electron microscopy, Stone and Broome (1975) found a way to distinguish the two New

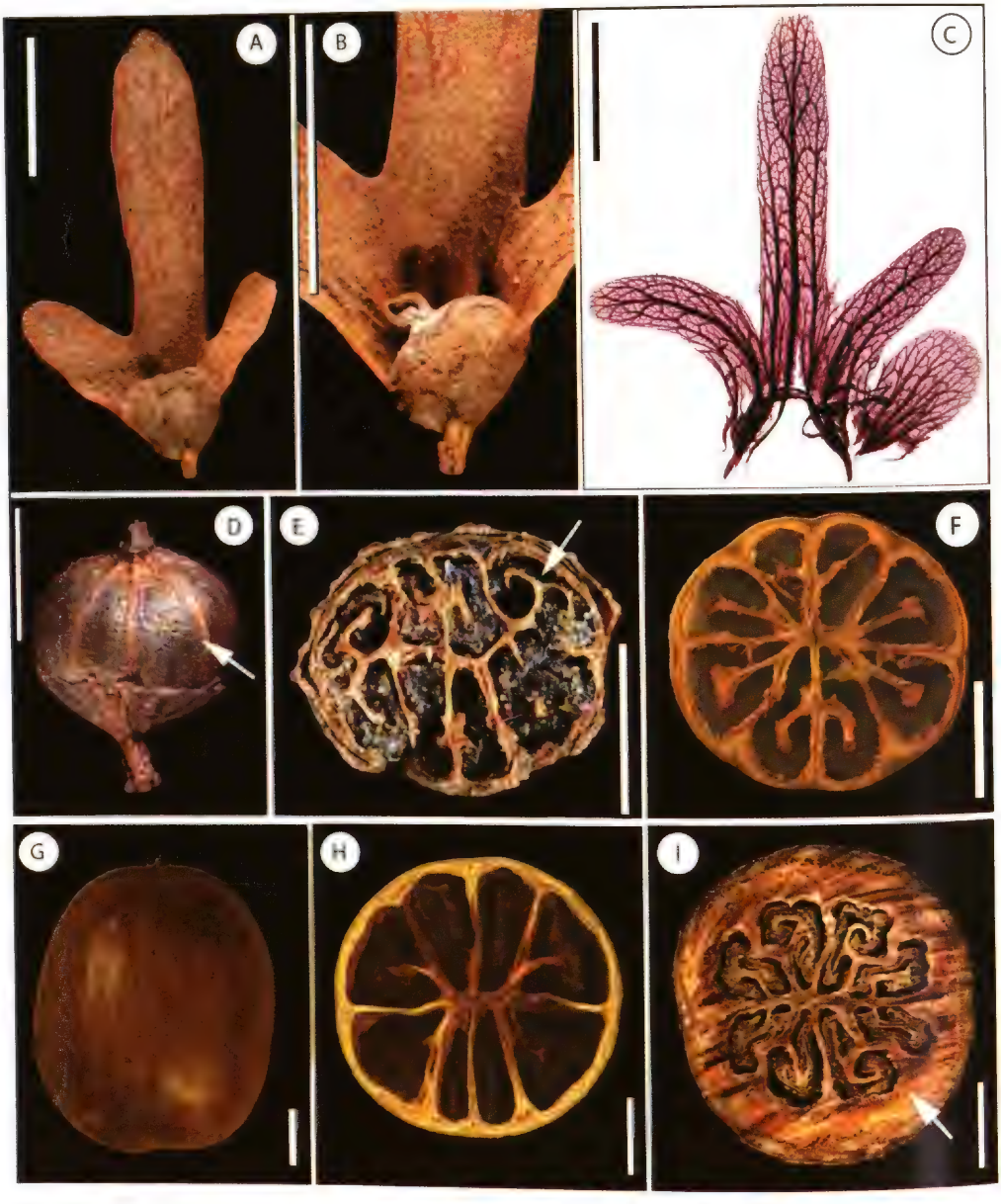

FIGURE 2. Extant fruits of *Oreomunnea* and *Alfaroa*. A–E. *Oreomunnea mexicana*. —A. Three-lobed wing for fruit dispersal. —B. Close-up from A; nut with two short styles. —C. Cleared wing with three major veins in lobes. —D. Lateral view of nut showing strands of fibers (arrow). —E. Equatorial cross section of nut; locule divided by primary and secondary septa into eight compartments, four on each side of the straight primary septum, and Y-shaped bifurcated septum (arrow). —F. *Oreomunnea pterocarpa*, equatorial cross section of nut; locule with eight compartments. G, H. *Alfaroa williamsii*. —G. Lateral view of nut. —H. Equatorial cross section of nut; locule with eight compartments and inconspicuous bifurcations of septa. —I. *Alfaroa guatemalensis*, equatorial cross section of large nut; locule with eight compartments and conspicuous bifurcations of septa. A, B, D, E, *Stone 2141*; C, *UF1312*; F, *Stone 134*; G, H, *Stone 2210*; I, *Stone 2999*. Scale bars: A–C, G–I = 1 cm; D–F = 0.5 cm.

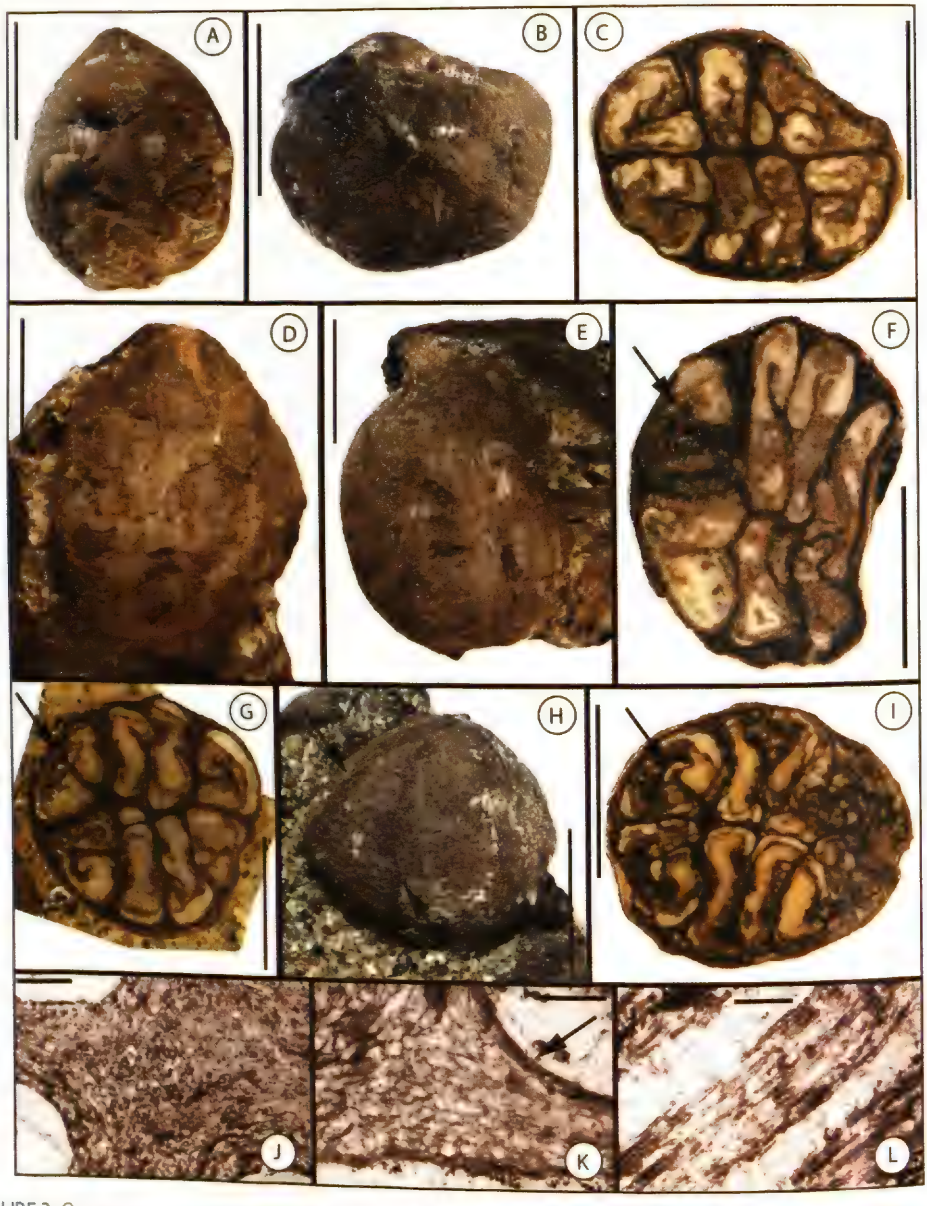

FIGURE 3. *Oreomunnea grahamii* Manch. & Herrera. A–C. Holotype UF621-59109. –A. Lateral view of nut. —B. Apical view of nut. —C. Equatorial cross section of nut; locule divided by primary and secondary septa into eight compartments, four on each side of the straight primary septum. —D. Paratype UF621-59110, lateral view of nut. E, F. Paratype UF621-59111. —E. Lateral view of nut. —F. More or less compressed specimen showing equatorial cross section and conspicuous Y-shaped bifurcated septum (arrow). —G. Paratype UF621-59108, more or less circular nut in cross section; arrow showing one of the eight compartments of the locule. H, I. Paratype UF621-59112. —H. Lateral view of nut showing strands of thick and dark fibers (arrows). —I. Equatorial cross section showing conspicuous Y-shaped bifurcated septum (arrow). J–L. Peel acetates from paratype UF621-59108. —J. Primary septum showing anisodiametric cells and abundant strands of fibers. —K. Close-up of secondary septum; fiber cells appear darker and thicker near the edge of septum (arrow). —L. Strand of long fiber cells. Scale bars: A–I = 0.5 cm; J–L = 200 μm.

Paratypes: designated here: UF00621-59110 (Fig. 3D), UF00621-59111 (Fig. 3E, F), UF00621-59108 (Fig. 3G, J–L), UF00621-59112 (Fig. 3H, I).

Type locality: Lirio East Outcrop, Gaillard Cut, southeastern Panama Canal (9°3′20″N, 79°39′40″W).

Stratigraphy and age: Lower Cucaracha Formation, Early Miocene.

Etymology: This species is named in honor of Alan Graham for his research contributions on the study of Neotropical floristic history.

Diagnosis: Nuts ovoid, elliptical in cross section, 8.3–10.1 mm long, 8.2–9.6 mm wide, 6.6–7.8 mm deep, rounded basally, pointed apically (Fig. 3A, B, D, E, H), smooth at the surface but with more or less conspicuous bands of dark and thick fibers (Fig. 3H), these bands separated from each other by 0.35–0.45 mm near the equator. In equatorial cross sections, the nut appears divided by primary and secondary septa, creating 8 compartments, 4 on each side of the straight primary septum (Fig. 3C, F, G, I). Each compartment intruded by an additional partial septum, straight or curved, often bifurcated in the shape of a Y in the 4 exterior compartments as seen in cross section. Nutshell 0.11–0.56 mm thick, septa 0.10–0.89 mm thick, composed of anisodiametric cells (13–71 µm in diameter; Fig. 3J, K) and abundant strands of fibers (>900 µm long and 13–19 µm thick; Fig. 3L), fiber cells appear darker and thicker near the edge of the septa (Fig. 3K).

Taxonomic affinity of the fossil: The subdivision of the nut by primary and secondary septa into eight compartments is a feature found only in *Oreomunnea* and *Alfaroa*. Other Juglandaceae have two main compartments divided by a primary septum, or four subcompartments formed by the intersection of secondary and primary septa. In Juglandaceae, the primary septum arises from the base of the ovary and extends nearly but not completely to the apex. The single seed is thus deeply lobed from the base. The secondary septa also arise from the base and are usually oriented at right angles to the primary septum. In some taxa secondary septa do not develop, and in most genera they extend only about half of the distance to the apex; however, in *Oreomunnea* and *Alfaroa* they extend half or more the distance to the apex. The predominantly fibrous composition of the septa and nutshell is a feature shared by members of the Engelhardioideae subfamily that distinguishes them from other Juglandaceae, in which the septa and nutshell are mostly composed of isodiametric sclereids. The extinct engelhardioid genus, *Beardia* Elliott, Stockey & Mindell, from the Middle to Late Eocene of Vancouver Island, British Columbia, had a thick husk and a nutshell composed of fibers (Elliott et al., 2006). It appears to have been wingless, like *Alfaroa*, but transverse sections of that fossil show that the fruit was divided into four compartments at the base and two at the equatorial section, contrasting with the eight-compartmented nuts of *Alfaroa* (Elliott et al., 2006).

One of the main characters separating *Oreomunnea* and *Alfaroa* is the presence of dispersal wings on the former (Fig. 2A–C). The Panamanian fossils lack evidence of attached wings (Fig. 3), but this does not mean that they were wingless in life. The coarse, high-energy sediments in which these fossils are preserved are suitable for preservation of wood, fruits, and seeds, but they rarely preserve leaves and other laminar organs. Size and shape of nuts is another feature that helps to distinguish these two genera. Lengths and widths of the fruits in extant *Alfaroa* species (Fig. 2G–I) range from 2.0 × 1.5 cm in *A. williamsii* Ant. Molina to 6.5 × 3.35 cm in *A. guatemalensis* (Standl.) L. O. Williams & Ant. Molina (D. E. Stone, unpublished data). On the other hand, *Oreomunnea* nuts (Fig. 2D–F) range from 0.5 cm in *O. mexicana* (Standl.) J.-F. Leroy to 1.1 × 1.3 cm

in *O. pterocarpa* Oerst. The size of the Cucaracha fossils, 0.8–1 cm long, and 0.7–0.9 cm in equatorial diameter, is significantly smaller than those of extant *Alfaroa* species and consistent with the range in extant *Oreomunnea*. In addition, the thickness of the nutshell and septa highly contrast between the two extant genera. In *Oreomunnea*, nutshell and septa thickness varies from ca. 0.1–0.5 mm, while in *Alfaroa* thickness varies from ca. 0.5–7.3 mm (Fig. 2E, F, H, I). Based on nut size and nutshell and septa thickness, the Panamanian fossils thus conform to *Oreomunnea*.

DISCUSSION AND IMPLICATIONS

Dilcher et al. (1976) described a winged fruit from the Eocene of Tennessee as *Paraoreomunnea* Dilcher, Potter & Crepet, which showed wing venation similar to that of *Oreomunnea* fruits and fragmentary carbonized fruit remains that were possibly eight-compartmented (Dilcher et al., 1976: fig. 22), but those fossils are not permineralized and the compression material is too fragmentary to be sure about the number and position of septa. Manchester (1987) transferred this and other fossil winged fruits with *Engelhardia*- and *Oreomunnea*-like trilobate wings from the North American, European, and Asian Tertiary to *Palaeocarya* Saporta, because many of the fossil occurrences show a combination of characters that is not completely confined to one modern genus or the other. In Europe, and in most North American localities, the venation of the bracts (with three strongly ascending veins in each lobe) resembles that of *Oreomunnea*, but the associated nutlets are only two- to four-celled (Manchester, 1987). The Tennessee fossil *Palaeocarya puryearensis* (Berry) Manchester appears to represent the closest extinct taxon to *Oreomunnea* (assuming that the eight-compartment interpretation of the nutlet is correct), or it may belong on the stem lineage of the *Oreomunnea–Alfaroa* clade. The fossil fruits of *P. puryearensis* have a bilobed prophyllum (Manchester, 1987: fig. 24A, B) unlike the rounded, unlobed prophyllum of extant species of *Oreomunnea*. Dilcher and Manchester (1986) studied associated compound juglandaceous leaves from the Eocene of western Tennessee and concluded that they showed similarity both to *Oreomunnea* and *Alfaroa*, and therefore assigned them to a fossil genus, *Oreoroa* Manch. & Dilcher.

The pollen records of Graham indicate that the Engelhardioideae clade was present already in the Eocene Gatuncillo Formation and extended to the Miocene of the Culebra (formerly treated as La Boca by Graham, 1989) and Cucaracha formations, but we do not know if those Eocene populations corresponded to one of the extant genera, or to an extinct related genus. In the Eocene of Tennessee, four distinct genera of winged engelhardioid fruits were present, all of which are thought to have had triporate, isopolar pollen similar to that of the extant genera. These were *Paraengelhardtia* Berry, with a small nut and shallowly trilobed wing; *Paleooreomunnea* Dilcher, Potter & Crepet, with a very large bilobed nut and shallowly trilobed wing; *Engelhardia mississippiensis* Berry, with a deeply trilobed wing having venation similar to that of extant *Engelhardia*; and *Palaeocarya*.

The *Oreomunnea grahamii* fruits considered here provide resolution to the generic level, permitting recognition of *Oreomunnea* in the Central American fossil record for the first time. It is possible that *Alfaroa* and *Oreomunnea* represent a radiation that was confined to the Neotropics. Although we still do not have unequivocal fossil evidence for the genus *Alfaroa*, this fossil confirms that the eight-celled condition, regarded here as a synapomorphy of the *Alfaroa–Oreomunnea* clade, was present about 20 Ma in Panama.

The *Oreomunnea* fruits are just one component of the permineralized Cucaracha fruit and seed flora currently under study (Herrera et al., 2012). Other disseminule elements include Anacardiaceae (*Spondias* L., *Pentoperculum* Manch.), Annonaceae, Arecaceae, Cannabaceae, Chrysobalanaceae (cf. *Parinari* Aubl.), Euphorbiaceae, Fabaceae, Hu-

miriaceae (*Sacoglottis* Mart.; Herrera et al., 2010), Icacinaceae (Phytocreneae tribe), Lauraceae, Menispermaceae, Myristicaceae, Passifloraceae, and Vitaceae (*Cissus* L.). Silicified woods from the same level include Annonaceae and Malvaceae (Rodriguez-Reyes & Falcon-Lang, 2011). This megafossil flora indicates a strong representation by angiosperms and emphasizes the woody component of the flora—mainly trees, shrubs, and lianas, contrasting with the Cucaracha palynoflora (Graham, 1988b), which included a high proportion of fern spores. As comparative studies of the fossil and extant fruits continue, we expect to expand our understanding of the vegetation to which *O. grahamii* belonged. Extant *Oreomunnea* grows in forests of medium to high elevation in Central America; if *O. grahamii* grew in similar ecological settings, the new fossils may be an indicator of the Early Miocene topographic relief in Panama, which is also suggested by recent exhumation using Zircon thermochronology (Farris et al., 2011; Montes et al., 2012a, 2012b).

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PALYNOLOGICAL RECORD OF THE LAST 20 MILLION YEARS IN PANAMA

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ABSTRACT

The Isthmus of Panama illustrates how the vegetation of a newly created landscape in a tropical setting evolves over time. It also allows us to investigate biological invasions, because the landscape was first connected to temperate North America, and later connected to tropical South America. Using a large number of outcrops newly exposed during the recent expansion of the Panama Canal, we were able to complement the extensive palynological research that Alan Graham conducted in Panama over the past 25 years. We analyzed the palynological record of the interval 19.5–1.2 Ma, represented by 282 samples containing 27,910 grains (pollen/spores) with 496 morphotypes. Further, a revision of the plant macrofossil literature of Panama and analysis of the carbon isotope content of 14 samples were carried out. Our results indicate that since the Early Miocene, Panamanian forests have been dominated by Gondwana-Amazonian taxa, suggesting that plants were able to cross the Central American Seaway much earlier than mammals. The landscape was dominated by tropical rainforest and lower montane to montane forest, contrary to the dry and open habitats that some previous studies have proposed. Plant diversity seems to have increased over the past 10 My, but it is unclear if this increase is due to a taphonomic bias. Further studies are needed to understand the relationships of the Early Miocene Panamanian mammals derived from North American temperate forest lineages as they faced new habitats in Panama dominated by South American–derived tropical rainforest.

Key words: biogeography, GABI, Neogene, paleobotany, palynology.

A century ago, during the initial excavations for the Panama Canal, the Smithsonian Institution conducted intensive natural history and geological investigations, resulting in some of the first major collections that documented the high biodiversity of the American Neotropics (e.g., Vaughan, 1919). Almost a century later, starting in 2007, after a public referendum, the government of Panama decided to widen the Panama Canal. The $5 billion project is scheduled for

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completion in 2014. The Smithsonian Tropical Research Institute and the University of Florida have taken advantage of this extraordinary opportunity to collect fossils and geological information to better understand the uplift of the Isthmus of Panama, which had far-reaching biological, climatic, and tectonic implications. The recently exposed rocks have allowed us to compile large amounts of new geological and paleontological data that otherwise would have been impossible to collect, given that most of the Panamanian landscape is covered by tropical rainforest. Many highly fossiliferous sedimentary strata were exposed, giving us a glimpse of the evolution of the landscape, the formation of the isthmus, and the ecosystem, flora, and biota of Panama during the past 20 million years.

The Panamanian fossil vertebrate collections provide a good record of Miocene North American mammal immigrants, including horses, bear-dogs, camels, rhinocerids, peccaries, and rodents (Whitmore & Stewart, 1965; Slaughter, 1981; MacFadden & Higgins, 2004; MacFadden, 2006a, 2006b, 2009, 2010; MacFadden et al., 2012; Rincon et al., 2012, 2013); South American immigrants include turtles, snakes, and crocodiles (Cadena et al., 2012; Head et al., 2012; Hastings et al., 2013). The geological history of the Isthmus of Panama can be divided broadly into four segments (Coates et al., 1992, 2003, 2004; Coates & Obando, 1996; Farris et al., 2011; Montes et al., 2012a, 2012b; Sepulchre et al., 2014): (1) a pre-22 Ma interval during which most of Panama was underwater, except some Late Eocene and Oligocene volcanic islands; (2) an initial collision with South America around 22–21 Ma with an associated broad-scale land exhumation and a narrowing of the Central American Seaway (CAS) to ca. 200 km (CAS is defined here as the oceanic seaway along the tectonic boundary of the South American plate and the Panamanian microplate); (3) a final and major exhumation at 12–10 Ma, when most of the Panamanian landscape was exhumed above sea level and the CAS was fully closed, ending deep and intermediate water exchange between the Caribbean and Pacific; (4) an intermittent exchange between 10 and 3.5 Ma of shallow waters between the Pacific and the Caribbean (Coates et al., 1992; Coates & Obando, 1996; Haug & Tiedemann, 1998) along places other than the CAS. At 4.2–3.5 Ma a full closure of the isthmus occurred (Coates et al., 1992; Haug et al. 2001, 2004). The complete isthmus formation facilitated exchange of faunas and floras of South America with those of Central and North America, in a process that has been named GABI (the Great American Biotic Interchange; Stehli & Webb, 1985; Coates & Obando, 1996). Modern Neotropical biodiversity and biogeographic distributions are deeply affected by this interchange.

Our study presents an overall view of the vegetation evolution of the isthmus for the past 20 My, using both palynological and macrofossil data. We attempt to answer four questions, namely: (1) what are the vegetation types that have dominated the Isthmus of Panama over the past 20 Ma?, (2) are there any lines of evidence for widespread savannas or dry forests?, (3) what is the biogeographic origin of the floras found in Panama?, and (4) how has plant diversity changed? In particular, we hypothesized that the earlier floras would have been dominated by North American (Laurasian) families, due to the relatively late physical connection with South America brought on by full closure of the isthmus at ca. 3.5 Ma.

This investigation was based on the analysis of 282 palynological samples together with the extensive palynological research of Dr. Alan Graham on Panamanian sedimentary formations (Graham, 1977, 1988a, 1988b, 1989, 1991a, 1991b, 1991c, 1992, 1995, 1999, 2010, 2011). Our palynological work focused on the Cucaracha, Culebra, Gatun, and Chagres formations that outcrop along the canal in central Panama, together with samples from western Panama (Bocas del Toro) and eastern Panama (Darien). Macrobotanical in-

formation is derived from newly discovered fossil assemblages (leaves, fruits, and wood) from the Cucaracha and Gatun formations, together with a review of previous published work.

GRAHAM CONTRIBUTIONS

Graham has been a pioneer in the study of the floristic evolution of Central America and the Caribbean, publishing extensively across many regions and time periods. See Graham (2010, 2011) for an excellent synthesis of his impressive research over the past 40 years. In a series of papers, he described the palynofloras of central Panama, including La Boca, Culebra, Cucaracha, and Gatun formations. His study of La Boca Formation (Graham, 1989), was not included here because the precise stratigraphic position of this site in relation to our stratigraphic work could not be determined, and it could correspond to the Lower Culebra or Cascadas formations. The original site, which is in an area with high structural complexities, no longer exists, since it was depleted before our study in the Panama Canal started.

From the La Boca Formation (Graham, 1989), Graham found 54 morphotypes, including 39 where natural affinities could be assessed. The sediments were mostly marine, and some samples were dominated by mangrove elements (*Rhizophora* L.) and some dinoflagellates. The flora reflects low-lying volcanic islands fringed by mangroves, with freshwater and palm swamp, marshes, and tropical wet/moist and premontane forest. There is no evidence of dry habitats, including savannas or high elevations (> 1500 m). The flora is similar to extant coastal Panamanian floras. Climate was humid-tropical, similar to that of modern southern Central America.

Study of the Culebra Formation (upper Culebra) (Graham 1987, 1988b), where 41 palynomorphs were identified, indicated an estuarine sequence. Ferns constitute 25% of the flora, palms 4%, and lowland vegetation 71%. Tropical moist forest, represented by 30 genera, dominated the assemblages of premontane wet forest (25 genera), tropical wet forest (22 genera), and some forms of premontane moist forest (12 genera). Communities of higher elevations and dry to arid habitats (including savannas) are poorly represented to absent. Climate was similar to modern Panama, with 2.7–3.2 m rainfall annually, and tropical temperatures. All 41 taxa identified are still represented in the modern flora of Panama.

The study of the Cucaracha Formation (Graham, 1988a) identified 19 palynomorphs accumulated in an estuarine sequence. Paleocommunities included fern/palm marshes, mangroves, tropical wet/moist forests, and premontane forests. There is no evidence for high-altitude (> 1500 m) vegetation or dry vegetation (savanna). The affinity of the palynoflora showed connection to North American and Central American floras, and paleoclimatic conditions were interpreted as similar to modern Panama (tropical temperatures and high levels of rainfall). Graham (1988a) proposed that the volcanic activity might have produced disruptions in the vegetation, with resulting short-term open communities (savannas) that are suggested by the presence of browsers and grazers in the mammalian faunas of the Cucaracha Formation.

Graham (1991a, 1991b, 1991c) dated the Gatun Formation as Middle Miocene, but more recent work has indicated a Late Miocene age (Hendy, 2013). Graham identified 110 palynomorphs from several habitats, including shallow marine communities, mangroves, freshwater swamps/marshes, tropical wet/moist forests, premontane rainforests/moist forests, lower montane moist forests, and tropical dry forest. There was an increase in diversity compared to earlier floras, an increase of grasses (but only up to 7.5%), more developed dry forest, better representation of lower montane forest, and possibly, the first indication of differentiation between a wetter Atlantic side and a drier Pacific side in Panama.

VEGETATION TYPES IN THE ISTHMUS OF PANAMA

Today there are several types of forests in Panama, reflecting a variety of environmental differences—mainly differences in the mean annual precipitation (MAP) and the amount of precipitation during the dry season. Forests include lowland wet forest (> 300 mm of rain during the dry season), seasonal lowland moist forest (100–300 mm during the dry season), and lowland dry forest (≤ 1600 mm MAP and ≤ 100 mm during the dry season) (Pyke et al., 2001; Condit et al., 2004). The Caribbean side is also much wetter than the Pacific side. Additional forest types include swamp forest, seasonally flooded riparian forest, mangrove forest, and montane and premontane forests. An extensive review of each of those forest types has been provided by Graham in a number of seminal works in the past few years (Graham, 1991c, 2010). We have used his vegetation classification approach to assess the types of forest found in the fossil record (Table 1).

METHODS

SAMPLES

A total of 282 palynological samples were analyzed. Samples came from three sources: (1) Fifty-five samples were from a measured and described stratigraphic section of the full span of Culebra and Cucaracha formations from the new excavations of the Panama Canal (Emperador section for the Lower Culebra, and Hodges Hill section for the Upper Culebra and Cucaracha) (Figs. 1, 2, Table 2). (2) Two hundred samples previously collected by the Panama Paleontology Project (PPP) (Collins & Coates, 1999) were processed for palynological analyses. These were collected from central Panama (from Gatun and Chagres formations), eastern Panama (Darien region), and western Panama (Bocas del Toro) (Figs. 1, 2, Table 2). (3) Palynological information previously published by Graham (1987, 1988a, 1988b, 1991a, 1991b, 1991c) was added to our stratigraphic framework (Montes et al., 2012b; Hendy, 2013), including 11 samples from the Culebra Formation, seven samples from the Cucaracha Formation, and nine samples from the Gatun Formation (Figs. 1, 2, Table 2). The stratigraphic position as well as the label of each sample is given in the Supplementary Appendix (<http://dx.doi.org/10.5479/data.stri.jaramillo-2014>). Palynological samples were prepared by digesting 30 g of sediment in HCl and HF, then oxidizing if necessary (Traverse, 2007), and all slides were added to the Alan Graham Palynological Collection, the extensive pollen collection donated by Alan Graham to the Smithsonian Institution a few years ago.

AGE

The age for the Culebra and Cucaracha has been estimated as 19.5–18.5 Ma using uranium-lead (U-Pb) geochronology and magnetostratigraphy (MacFadden et al., 2012; Montes et al., 2012a, 2012b): 19.5–19 Ma for Culebra Formation and 19–18.5 Ma for Cucaracha Formation. For the age of individual samples within these formations, a linear and constant accumulation rate was assumed, since there are no major lithological changes within each formation (Supplementary Appendix). Age for each PPP sample has been determined using planktonic foraminifera and calcareous nannoplankton (Collins & Coates, 1999). Ages of 12 to ca. 8.5 Ma (Middle to Late Miocene) for the Gatun Formation and 6.5–5.5 Ma (Late Miocene) for the Chagres Formation have been determined using foraminifera, nannoplankton, and molluskan biostratigraphy (Collins & Coates, 1999; Hendy, 2013). See Figures 1, 2, Table 2, and Supplementary Appendix.

ECOLOGICAL PREFERENCES AND BIOGEOGRAPHIC ORIGINS

Ecological preferences for fossil taxa follow mainly Graham (1991c), with additional input (Germeraad et al., 1968; Croat, 1978; Henderson et al., 1995; Correa & Valdespino, 1998; March-

TABLE 1. Ecological preferences for fossil taxa, based primarily on Graham (1991c), with additional input from Germeraad et al. (1968), Croat (1978), Henderson et al. (1995), Correa and Valdespino (1998), Marchant et al. (2001), Correa et al. (2004), Carrasquilla (2006), and Henderson (2011).

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Acacia Mill.								
Acalypha diversifolia Jacq.								
Aegiphila Jacq.								
Alchornea Sw.								
Alfaroa Standl.								
Alfaroa/Oreomunnea Standl./Oerst.								
Allophylus L.								
Alnus Mill.								
Alsophila R. Br.								
Amanoa Aubl.								
Bernoullia Oliv.								
Bombacopsis Pittier								
Borreria G. Mey.								
Bucida L.								
Bucida L.								
Bursera Jacq. ex L.								
Cabomba Aubl.								
Caesalpinia L.								
Casearia Jacq.								
Catopsis Griseb.								
Cayaponia Silva Manso								
Cedrela P. Browne								
Ceiba Mill.								
Ceratopteris Brongn.								
cf. *Aguiaria* Ducke								
cf. *Cionosicys* Griseb.								
cf. *Glycydendron* Ducke								
cf. *Jatropha* L.								
cf. *Stillingia* Garden ex L.								
cf. *Jatropha* L.								
Chelonanthus (Griseb.) Gilg								
Chomelia Jacq.								
Chrysophyllum L.								
Cnemidaria C. Presl								
Combretum Loefl.								
Combretum Loefl./*Terminalia* L.								
Cordia L.								
Cosmibuena Ruiz & Pav.								
Crudia Schreb.								
Cryosophila Blume								
Ctenitis (C. Chr.) C. Chr.								
Cupania L.								

TABLE 1. (*continued*)

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Cyathea Kaulf.								
Cymbopetalum Benth.								
Danaea Sm.								
Desmoncus-type Mart.								
Dinoflagellates								
Dioclea reflexa Hook. f.								
Dioscorea L./*Rajania* L.								
Doliocarpus Rol.								
Erythrina L.								
Eugenia L.								
Eugenia L./*Myrcia* DC.								
Euterpe Mart.								
Faramea Aubl.								
Foram lining								
Genipa americana L.								
Glycydendron Ducke								
Gomphrena L.								
Grammitis Sw.								
Guarea F. Allam. ex L.								
Hampea Schltdl.								
Hampea Schltdl./*Hibiscus* L.								
Hauya DC.								
Hedyosmum Sw.								
Hemitelia R. Br./*Cnemidaria* C. Presl								
Hibiscus L.								
Humiria Aubl.								
Ilex L.								
Iriartea deltoidea Ruiz & Pav.								
Jamesonia Hook. & Grev.								
Jatropha L.								
Ludwigia L.								
Lycopodium L.								
Lygodium Sw.								
Lygodium microphyllum (Cav.) R. Br.								
Machaerium Pers.								
Manicaria-type Gaertn.								
Matayba Aubl.								
Mauritia L. f.								
Mauritia flexuosa L. f.								
Miconia Ruiz & Pav.								
Monolete fern spore types 1-2 (Blechnaceae)								
Mortoniodendron Standl. & Steyerm.								
Mutisieae type Cass.								

(*continued*)

TABLE 1. (*continued*)

Taxa	TRFO	PMF	MF	TDFO	SV	FW	MG	MR
Myrcia DC.								
Oenocarpus Mart.								
Ophioglossum L.								
Oryctanthus (Griseb.) Eichler								
Pachira aquatica Aubl.								
Palmae type 1								
Paullinia L.								
Pelliciera Planch. & Triana								
Petrea L.								
Phytelephas Ruiz & Pav.								
Poaceae								
Podocarpus L'Hér. ex Pers.								
Polypodiaceae/Pteridaceae								
Posoqueria Aubl.								
Pouteria Aubl.								
Protium Burm. f.								
Pseudobombax Dugand								
Psidium L.								
Pteris L.								
Quercus L.								
Rhizophora L.								
Rourea Aubl.								
Sabicea Aubl.								
Sapium Jacq.								
Sapium caudatum Pittier								
Scheelea zonensis L. H. Bailey								
Selaginella P. Beauv.								
Serjania Mill.								
Serjania cf. Mill.								
Spondias L.								
Stenochlaena palustris (Burm. f.) Bedd.								
Stillingia Garden ex L.								
Symphonia globulifera L. f.								
Symplocos Jacq.								
Tetrorchidium macrophyllum Müll. Arg.								
Trichilia P. Browne								
Utricularia L.								
Vernonia Schreb.								
Vochysia Aubl.								

Abbreviations: TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community.

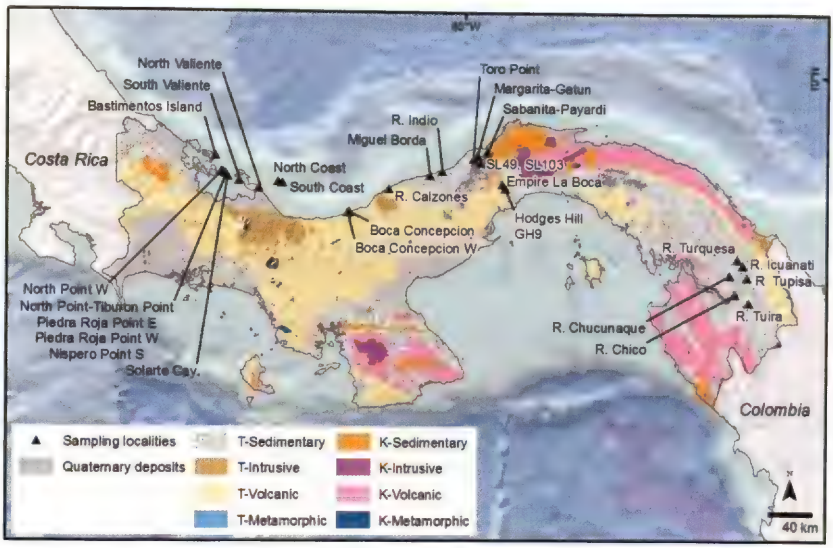

FIGURE 1. Sampling localities displayed on Panama's regional geology. "North Coast" and "South Coast" localities are on Escudo de Veraguas Island. Geology is from the National Environmental Authority (ANAM). Elevation data are from the Shuttle Radar Topography Mission (U.S.G.S., 2004) and bathymetry is from the ETOPO1 dataset (Amante & Eakins, 2009).

ant et al., 2001; Correa et al., 2004; Carrasquilla, 2006; Henderson, 2011) (Table 1).

For biogeographic origins, we followed the approach of Gentry (1982). Plant families were given a biogeographic origin provided by Gentry, including Gondwana-Amazonian families, Gondwana-northern Andean, Gondwana-southern Andean, Laurasian, or unassigned (Table 3). Modern vegetational abundance data and species composition were derived from the 50-ha plot of Barro Colorado Island in Panama (Condit et al., 2004) (Appendix 1). The data from this plot include approximately 240,000 stems of 303 species of trees and shrubs more than 1 cm in diameter at breast height, representing ca. 96% of the biomass in the plot (Chave et al., 2003, 2005). Pollen traps in the soil within the plot also have shown than pollen spectra produce a representative sample of the vegetation within the plot (Bush & Rivera, 1998; Haselhorst et al., 2013), consequently making the pollen record a good proxy to understand the forest.

STABLE CARBON ISOTOPES

We used stable carbon isotopes to identify C3 versus C4 photosynthetic pathways, as a means to identify the presence of C4 savannas (rich in C4 grasses) versus trees (C3). Sediment samples were freeze-dried and crushed with a mortar and pestle. Total carbon and total nitrogen were measured using a Carlo Erba (Milan, Italy) NA1500 CNS elemental analyzer with a zero blank autosampler. Carbonate carbon was determined by coulometric titration using an automated acidification prep device coupled with a UIC CO2 coulometer. Percentage of organic carbon was calculated by subtraction of carbonate carbon from total carbon. Samples for isotopic analyses were treated with 2 N HCl to remove carbonate and then washed with distilled water to remove chloride. Approximately 50 mg of carbonate-free bulk sediment was loaded into tin sample capsules and placed in a 50-position automated sample zero blank carousel on the elemental analyzer. Combustion gases were carried in a helium stream through

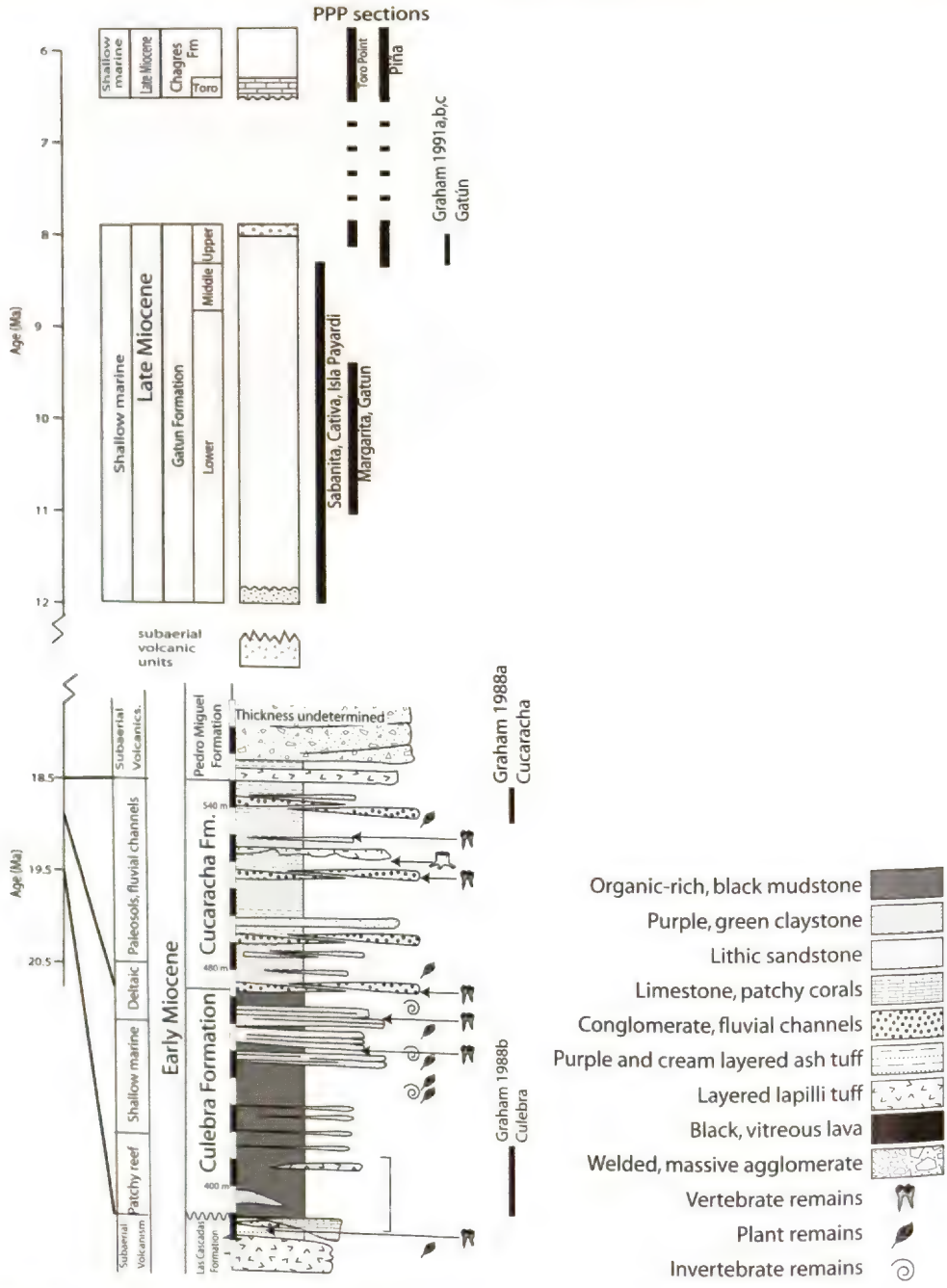

FIGURE 2. Stratigraphic profile of the main formations and sections studied in central Panama. Stratigraphy and age of Cucaracha and Culebra formations after Montes et al. (2012b) and MacFadden et al. (2012); Gatun Formation after Hendy (2013). PPP = Panama Paleontology Project.

TABLE 2. Geographical location of the studied samples.

Region	Section name	Formation name	Latitude	Longitude	Source
Central Panama	Empire section La Boca	Culebra	9.0827	–79.6789	this study
Central Panama	Hodges Hill section	Culebra/Cucaracha	9.05	–79.6534	this study
Central Panama	01-Sabanita to Payardi	Gatun	9.351083333	–79.808	PPP samples
Central Panama	02-Margarita to Gatun	Gatun	9.32575	–79.89133333	PPP samples
Central Panama	03-Toro point	Gatun	9.296083333	–79.92466667	PPP samples
Central Panama	05- Rio Indio	Chagres	9.192138889	–80.19133333	PPP samples
Central Panama	06-Miguel de la Borda	Gatun	9.154833333	–80.29133333	PPP samples
Central Panama	07-Boca de Concepcion	Gatun	8.847583333	–80.97466667	PPP samples
Central Panama	08-Boca de Concepcion West	Gatun	8.841416667	–80.99133333	PPP samples
Central Panama	09 -Calzones River	Gatun	9.045083333	–80.64133333	PPP samples
Western Panama	10-North Coast	Escudo Veraguas	9.101444444	–81.57466667	PPP samples
Western Panama	11-South Coast	Escudo Veraguas	9.089944444	–81.54133333	PPP samples
Western Panama	12-North Valiente	Shark Hole Point	9.042777778	–81.74133333	PPP samples
Western Panama	15-South Valiente	Shark Hole Point	9.106666667	–81.908	PPP samples
Western Panama	16-North Point West	Cayo Agua	9.18	–82.058	PPP samples
Western Panama	17-Piedra Roja Point West	Cayo Agua	9.141083333	–82.008	PPP samples
Western Panama	18-Piedra Roja Point East	Cayo Agua	9.143138889	–82.008	PPP samples
Western Panama	19- North Point-Tiburon Point	Cayo Agua	9.174888889	–82.04133333	PPP samples
Western Panama	20-Nispero Point South	Cayo Agua	9.167527778	–82.02466667	PPP samples
Western Panama	22-Bastimentos Island	unnamed	9.317777778	–82.108	PPP samples
Western Panama	23-Bastimentos Island	unnamed	9.317277778	–82.108	PPP samples
Western Panama	24- Solarte Cay	unnamed	9.142194444	–82.008	PPP samples
Eastern Panama	Rio Chico	Tuira?	8.17075	–77.708	PPP samples
Eastern Panama	Rio Chucunaque	Chucunaque	8.331138889	–77.758	PPP samples
Eastern Panama	Rio Icuanati	Lara	8.410416667	–77.64133333	PPP samples
Eastern Panama	Rio Tuira	Tuira	8.097	–77.59133333	PPP samples
Eastern Panama	Rio Tupisa	Tuira	8.308611111	–77.608	PPP samples
Eastern Panama	Rio Turquesa	Tuira	8.465722222	–77.69133333	PPP samples
Central Panama	Core SL103	Gatun	9.266666667	–79.86666667	Graham, 1991c
Central Panama	Core SL49	Gatun	9.266666667	–79.86666667	Graham, 1991c
Central Panama	GH9	Culebra	9.05	–79.6534	Graham, 1988a
Central Panama	Roadside K2	Cucaracha	9.05	–79.6	Graham, 1988b

Abbreviation: PPP = Panama Paleontology Project.

a Conflo II interface to a Finnigan-MAT 252 isotope ratio mass spectrometer (PRISM). All carbon isotopic results are expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB).

PALYNOLOGICAL NOMENCLATURE

Morphological characteristics of the palynomorphs were compared with illustrations and descriptions from literature and summarized in Jaramillo and Rueda (2013). Major nomenclatural usages follow those in Jaramillo and Dilcher (2001). Informal species are those between quotation marks. In the taxonomic section (Appendix 2), 414 morphotypes are briefly described and/or illustrated. The taxa encountered and their counts are listed in the Supplementary Appendix,

TABLE 3. Biogeographic affinities after Gentry (1982) for the families present in either the Barro Colorado Island 50-ha plot or the fossil record presented in this report.

Biogeographic Province	Family
Dry area Gondwanan group	Erythroxylaceae
Gondwana-Amazonian	Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae, Bombacoideae, Burseraceae, Byttneroideae, Caesalpinioideae, Chrysobalanaceae, Combretaceae, Connaraceae, Dilleniaceae, Ebenaceae, Elaeocarpaceae, Euphorbiaceae, Fabaceae, Faboideae, Grewioideae, Humiriaceae, Lacistemataceae, Lauraceae, Lecythidaceae, Malpighiaceae, Meliaceae, Mimosoideae, Moraceae, Myristicaceae, Ochnaceae, Olacaceae, Phyllanthaceae, Polygalaceae, Rhizophoraceae, Sapindaceae, Sapotaceae, Simaroubaceae, Sterculiaceae, Tetrameristaceae, Tiliaceae, Violaceae, Vochysiaceae
Gondwana-northern Andean	Acanthaceae, Araceae, Araliaceae, Asteraceae, Bromeliaceae, Clusiaceae, Ericaceae, Loranthaceae, Monimiaceae, Nyctaginaceae, Piperaceae, Rubiaceae, Urticaceae
Gondwana-southern Andean	Bignoniaceae, Myrtaceae, Onagraceae, Podocarpaceae, Solanaceae
Laurasian	Achariaceae, Aquifoliaceae, Betulaceae, Boraginaceae, Celastraceae, Chloranthaceae, Fagaceae, Gentianaceae, Juglandaceae, Labiatae, Lythraceae, Melastomataceae, Rhamnaceae, Salicaceae, Staphyleaceae, Symplocaceae, Ulmaceae
Unassigned	Amaranthaceae, Cabombaceae, Cucurbitaceae, Cyperaceae, Dioscoreaceae, Dryopteridaceae, Lamiaceae, Lentibulariaceae, Malvaceae, Malvoideae, Nymphaeaceae, Picramniaceae, Poaceae, Polygonaceae, Rutaceae, Verbenaceae

as well as in Table 4, where possible natural affinities are provided. We employ a nomenclature using fossil names for each taxon, even when the natural affinities are known. This approach differs from that used by Graham in all his publications where the fossils were referred to extant families and genera when possible. We feel that using a fossil taxon naming approach would be more useful when comparing to fossil floras elsewhere in the tropics, where fossil morphotaxa have mostly been used. Also, using natural affinities as the name of a fossil taxon can bring nomenclatural problems in the future, because the affinity of a given fossil species can change when further research is done, specially using SEM and TEM. It would be more practical to have a fossil morphotaxon name with an informally suggested natural affinity; that is, a hypothesis of relationship can change over time, but the morphotaxon name will not.

DIVERSITY ANALYSES

A number of techniques were used to analyze the patterns of pollen and spore diversity and floral composition. Diversity is used here to denote the number of species (Rosenzweig, 1995). Diversity within a sample was estimated using rarefaction, an interpolation technique that estimates how many species may have been found if the sample had been smaller (Raup, 1975). The rarefaction was calculated with the fungal spores excluded because they can represent a large proportion of the palynological sum and thus can mask possible vegetation patterns; this exclusion from the diversity analyses was also appropriate, because little taxonomic work has been undertaken on Neotropical Neogene fungi.

Species accumulation curves (Gilinsky, 1991), using the collector method, were used to calculate how diversity increases as more samples are analyzed. The collector method adds sites in the order they happen to be in the data (Oksanen et al., 2010). It was used to compare the three time intervals that we analyzed (see below), because each interval represents a different time span, and comparison of them would have biased the diversity toward the interval with the longest duration (i.e., the longest duration interval would have a greater probability to accumulate more species).

TABLE 4. List of all species used in the analysis with their possible natural affinities. The Graham taxon name corresponds to the names used by Graham in his publications. Informal species are those within quotation marks.

Taxon	Category	Graham taxon name	Family	Genus
Acanthaceae aff. "hygrophilensis"	angiosperm		Acanthaceae	*Hygrophila*
Alnipollenites verus (Potonie, 1931) ex Potonie, 1934	angiosperm		Betulaceae	*Alnus*
Anacardiaceae "morenensis"	angiosperm		Anacardiaceae	*Spondias*
Anacardiaceae "sanchenzis"	angiosperm		Anacardiaceae	
Annonaceae (*Cymbopetalum*) Benth.	angiosperm	*Cymbopetalum*	Annonaceae	*Cymbopetalum*
Araceae type	angiosperm		Araceae	
Arecipites "perfectus"	angiosperm		Arecaceae	
Arecipites regio (Van der Hammen and Garcia, 1966) Jaramillo and Dilcher, 2001	angiosperm		Arecaceae	
Baculipollenites "inciertus"	angiosperm			
Bignoniaceae type	angiosperm		Bignoniaceae	
Bombacaceae (cf. *Aguiaria*) Ducke	angiosperm	cf. *Aguiaria*	Bombacoideae	*Aguiaria*
Bombacacidites "bombacopsiformis"	angiosperm		Bombacoideae	*Bombacopsis*
Bombacacidites "colpiechinatus"	angiosperm			
Bombacacidites "problematicus"	angiosperm			
Bombacacidites "pseudobombiformis"	angiosperm	*Pseudobombax*	Bombacoideae	*Pseudobombax*
Bombacacidites araracuarensis Hoorn, 1994	angiosperm	*Ceiba*	Bombacoideae	*Ceiba*
Bombacacidites baculatus Muller et al., 1987	angiosperm		Bombacoideae	*Pachira aquatica*
Bombacacidites brevis (Dueñas, 1980) Muller et al., 1987	angiosperm	Unknown Type 10	Bombacoideae	
Bombacacidites nacimientoensis (Anderson, 1960) Elsik, 1968	angiosperm	*Bernoullia*	Bombacoideae	*Bernoullia*
Brevitricolpites "panamensis"	angiosperm			
Brevitricolpites "triangulatus"	angiosperm	Unknown Type 9		
Brevitricolporites "scabratus"	angiosperm		Fabaceae	
Brevitricolpites sp. Gonzalez, 1967	angiosperm	Unknown Type 8		
Bromeliacidites sp. 1	angiosperm		Bromeliaceae	
Bromeliacidites sp. 2	angiosperm		Bromeliaceae	*Catopsis*
Burseraceae "protiumensis"	angiosperm		Burseraceae	*Protium*
Cabombaceae (*Cabomba*) Aubl.	angiosperm	*Cabomba*	Cabombaceae	*Cabomba*
Chelonanthus type (Griseb.) Gilg	angiosperm		Gentianaceae	*Chelonanthus*
Cichoreacidites longispinosus (Lorente, 1986) Silva-Caminha et al., 2010	angiosperm		Asteraceae	
Clavainaperturites clavatus Van der Hammen and Wymstra, 1964	angiosperm			
Clavainaperturites microclavatus Hoorn, 1994b	angiosperm		Chloranthaceae	*Hedyosmum*
Clavaperiporites "crotonoides"	angiosperm			
Clavapollenites "circularis"	angiosperm		Euphorbiaceae	
Clavapollenites "triangulatus"	angiosperm			
Clavatricolpites "infinitus"	angiosperm			
Clavatricolpites "tectatum"	angiosperm	*Tetrorchidium*	Euphorbiaceae	*Tetrorchidium*
Clavatricolpites sp. Van Hoeken Klinkenberg, 1964	angiosperm			
Colombipollis "guerrillensis"	angiosperm			

(continued)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Combretaceae (cf. *Bucida*) L.	angiosperm	cf. *Bucida*	Combretaceae	*Bucida*
Compositae (*Mutisieae* type) Cass.	angiosperm	Mutisieae type	Asteraceae	*Mutisieae*
Corsinipollenites psilatus Jaramillo and Dilcher, 2001	angiosperm		Onagraceae	*Ludwigia*
Crassiectoapertites columbianus Dueñas, 1980; emend. Lorente, 1986	angiosperm		Fabaceae	*Dioclea reflexa*
Cricotriporites "chagrensis"	angiosperm			
Cricotriporites "minimus"	angiosperm			
Cricotriporites aff. *macroporus* Jaramillo and Dilcher, 2001	angiosperm			
Crototricolpites "euphorbiensis"	angiosperm		Euphorbiaceae	
Crototricolpites "pseudodaemoni"	angiosperm			
Cucurbitaceae (cf. *Cionosicys*) Griseb.	angiosperm	cf. *Cionosicys*	Cucurbitaceae	*Cionosicys*
Cucurbitaceae type	angiosperm		Cucurbitaceae	*Cayaponia*
Cyperaceae	angiosperm		Cyperaceae	
Dioscorea L./*Rajania* L.	angiosperm	*Dioscorea/Rajania*	Dioscoreaceae	*Dioscorea-Rajania*
Echimonocolpites "dariensis"	angiosperm		Arecaceae	
Echimonocolpites "mauritiformis"	angiosperm		Arecaceae	
Echimonocolpites "mosquitensis"	angiosperm		Arecaceae	
Echimonocolpites "panamensis"	angiosperm		Arecaceae	*Mauritia*
Echiperiporites "aquaticus"	angiosperm			
Echiperiporites "ipomoensis"	angiosperm			
Echiperiporites "pantagruelicus"	angiosperm			
Echiperiporites akanthos Van der Hammen and Wymstra, 1964	angiosperm			
Echiperiporites estelae Germeraad et al., 1968	angiosperm	*Hampea/Hibiscus*	Malvoideae	*Hampea-Hibiscus*
Echiperiporites sp. Van der Hammen and Wymstra, 1964	angiosperm	Unknown Type 1		
Echistephanoporites "saggitarianus"	angiosperm			
Echitricolporites "chiquitinus"	angiosperm		Asteraceae	
Echitricolporites "devriesi"	angiosperm			
Echitricolporites "microspinosus"	angiosperm		Boraginaceae	*Cordia*
Echitricolporites "vesiculoides"	angiosperm	Compositae	Asteraceae	
Echitricolporites mcneillyi Germeraad et al., 1968	angiosperm		Asteraceae	*Ambrosia*
Echitricolporites sp. (Van der Hammen) Germeraad, Hopping & Muller 1968	angiosperm			
Echitricolporites spinosus Van der Hammen, 1956	angiosperm		Asteraceae	
Echitricolporites spinosus var. microspinosus	angiosperm		Asteraceae	
Echitriporites "abutiloensis"	angiosperm		Malvoideae	*Abutilon*
Echitriporites "megaexinatus"	angiosperm			
Echitriporites aff. "eocenicus"	angiosperm			
Ericaceae Type 1	angiosperm	Ericaceae Type 1	Ericaceae	
Ericaceae Type 2	angiosperm	Ericaceae Type 2	Ericaceae	
Ericipites "baculatus"	angiosperm		Ericaceae	
Ericipites "psilatus"	angiosperm	Ericaceae Type 2	Ericaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Erythrina L.	angiosperm	*Erythrina*	Fabaceae	*Erythrina*
Euphorbiaceae (cf. *Glycydendron*) Ducke	angiosperm	cf. *Glycydendrum*	Euphorbiaceae	*Glycydendron*
Euphorbiaceae (cf. *Jatropha*) L.	angiosperm	cf. *Jatropha*	Euphorbiaceae	*Jatropha*
Euphorbiaceae (cf. *Stillingia*) Garden ex L.	angiosperm	cf. *Stillingia*	Euphorbiaceae	*Stillingia*
Fagaceae (*Quercus*) L.	angiosperm	*Quercus*	Fagaceae	*Quercus*
Fenestrites "silanensis"	angiosperm		Asteraceae	
Fenestrites spinosus Van der Hammen, 1956	angiosperm		Asteraceae	*Vernonia*
Foveomonocolpites "panamensis"	angiosperm	*Desmoncus*-type	Arecaceae	*Desmoncus*
Foveostephanocolpites CU488	angiosperm	Unknown Type 4		
Foveotricolporites "brevicolpatus"	angiosperm			
Foveotricolporites "cingulatum"	angiosperm		Euphorbiaceae	*Sapium caudatum*
Foveotricolporites "colonensis"	angiosperm	*Doliocarpus*	Dilleniaceae	*Doliocarpus*
Foveotricolporites "longaporatus"	angiosperm			
Foveotriporites "bocencis"	angiosperm	Unknown Type 11 and 12		
Foveotriporites "ochromensis"	angiosperm			
Foveotriporites "protohammenii"	angiosperm	*Sabicea*	Rubiaceae	*Sabicea*
Gemmatricolporites sp. Leidelmeyer, 1966	angiosperm	Unknown Type 6		
Gemmatriporites "matisialis"	angiosperm			
Gomphrena sp. L.	angiosperm		Amaranthaceae	*Gomphrena*
Grimsdalea "aparecida"	angiosperm		Arecaceae	
Hauya DC.	angiosperm	*Hauya*	Onagraceae	*Hauya*
Heterocolpites "combretoides"	angiosperm		Combretaceae	*Combretum*
Heterocolpites "irregularis"	angiosperm		Melastomataceae	
Heterocolpites "melastomicus"	angiosperm		Melastomataceae	
Heterocolpites "minutus"	angiosperm		Melastomataceae	
Heterocolpites incomptus Hoorn, 1993	angiosperm		Melastomataceae	*Miconia*
Heterocolpites rotundus Hoorn, 1993	angiosperm	*Combretum*/ *Terminalia*	Combretaceae	*Combretum*-*Terminalia*
Heterocolpites sp. Van der Hammen, 1956	angiosperm			
Horniella "longicolpatus"	angiosperm			
Ilexpollenites "chiquitus"	angiosperm			
Ilexpollenites "clavavariatus"	angiosperm	*Ilex*	Aquifoliaceae	*Ilex*
Ilexpollenites "larguitus"	angiosperm		Aquifoliaceae	*Ilex*
Ilexpollenites "redonditus"	angiosperm			
Inaperturopollenites "crotonoides"	angiosperm			
Inaperturopollenites "grandiosus"	angiosperm			
Inaperturopollenites "reticulatus"	angiosperm	*Chomelia* type	Rubiaceae	*Chomelia*
Ladakhipollenites simplex (Gonzalez, 1967) Jaramillo and Dilcher, 2001	angiosperm			
Lanagiopollis crassa (Van der Hammen and Wymstra, 1964) Frederiksen, 1988	angiosperm		Tetrameristaceae	*Pelliciera rhizophorae*

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Leguminosae	angiosperm	Leguminosae	Fabaceae	
Lentibulariaceae	angiosperm	Lentibulariaceae	Lentibulariaceae	
Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall, 1967	angiosperm			
Longapertites "foveolatus"	angiosperm	*Cryosophila* type	Arecaceae	*Cryosophila*
Loranthaceae "atriensis"	angiosperm			
Loranthaceae "marginalis"	angiosperm		Loranthaceae	
Loranthaceae "oryctanthusis"	angiosperm		Loranthaceae	*Oryctanthus*
Loranthaceae Type 1	angiosperm	Loranthaceae Type 1	Loranthaceae	
Loranthaceae Type 2	angiosperm	Loranthaceae Type 2	Loranthaceae	
Magnastriatites grandiosus (Kedves and Sole de Porta, 1963) Dueñas, 1980	angiosperm	*Ceratopteris*	Pteridaceae	*Ceratopteris*
Malpighiaceae "bunchoensis"	angiosperm		Malpighiaceae	
Malpighiaceae Type 2	angiosperm	Malpighiaceae Type 2	Malpighiaceae	
Margocolporites "hematoxyformis"	angiosperm		Caesalpinioideae	*Caesalpinia*
Margocolporites "simpliporatus"	angiosperm			
Margocolporites vanwijhei Germeraad et al., 1968	angiosperm		Fabaceae	
Mauritiidites franciscoi var. *franciscoi* (Van der Hammen, 1956) Van Hoeken Klinkenberg, 1964	angiosperm		Arecaceae	*Mauritia flexuosa*
Mauritiidites franciscoi var. *minutus* Van der Hammen and Garcia, 1966	angiosperm		Arecaceae	
Melastomataceae	angiosperm	Melastomataceae	Melastomataceae	
Momipites "panamensis"	angiosperm	*Alfaroa/ Engelhardia*	Juglandaceae	*Alfaroa-Engelhardia*
Momipites africanus Van Hoeken Klinkenberg, 1966	angiosperm		Betulaceae	*Corylus*
Monocolpopollenites "canalensis"	angiosperm	*Synechanthus*-type	Arecaceae	*Synechanthus*
Monoporopollenites "minutus"	angiosperm		Poaceae	
Monoporopollenites annulatus (Van der Hammen, 1954) Jaramillo and Dilcher, 2001	angiosperm	Gramineae	Poaceae	
Multimarginites vanderhammenii Germeraad et al., 1968	angiosperm		Acanthaceae	*Sanchezia klugii*
Myrtaceae type	angiosperm		Myrtaceae	*Psidium*
Nymphaeaceae	angiosperm	Nymphaeaceae	Nymphaeaceae	
Ochnaceae type	angiosperm		Ochnaceae	
Onagraceae	angiosperm	Onagraceae	Onagraceae	
Pachydermites diederixi Germeraad et al., 1968	angiosperm		Clusiaceae	*Symphonia globulifera*
Palmae Type 1	angiosperm	Palmae Type 1	Arecaceae	
Palmapollenites "iriartoides"	angiosperm		Arecaceae	*Iriartea deltoidea*
Palmapollenites "microperforatus"	angiosperm	Palmae Type 2	Arecaceae	*Oenocarpus*
Palmapollenites "phytelephensis"	angiosperm		Arecaceae	*Phytelephas*
Palmapollenites "scheeleaensis"	angiosperm		Arecaceae	*Scheelea zonensis*

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Papilionoideae	angiosperm	Papilionoideae	Faboideae	
Parsonsidites "multiporatus"	angiosperm			
Perisyncolporites "gemmatus"	angiosperm			
Perisyncolporites pokornyi Germeraad et al., 1968	angiosperm	Malpighiaceae	Malpighiaceae	
Poloretitricolpites "centenarius"	angiosperm	*Pouteria*	Sapotaceae	*Pouteria*
Polyadopollenites "minutus"	angiosperm		Mimosoideae	*Acacia*
Polyadopollenites mariae Dueñas, 1980	angiosperm	*Acacia*	Mimosoideae	*Acacia*
Pouteria "mamey"	angiosperm			
Proteacidites triangulatus Lorente, 1986	angiosperm	*Allophylus*	Sapindaceae	*Allophylus*
Proxapertites "scabra?"	angiosperm		Araceae	
Proxapertites psilatus Sarmiento, 1992	angiosperm		Araceae	
Psilabrevitricolpites aff. *flexibilis* van Hoeken-Klinkenberg, 1966	angiosperm		Humiriaceae	
Psilabrevitricolporites "magnoporatus"	angiosperm			
Psilabrevitricolporites "vestibulatus"	angiosperm			
Psilabrevitricolpites aff. *rotundus* Van Hoeken-Klinkenberg, 1966	angiosperm		Apocynaceae	
Psilabrevitricolporites devriesi (Lorente, 1986) Silva-Caminha et al., 2010	angiosperm		Humiriaceae	*Humiria*
Psilabrevitricolporites triangularis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Sapindaceae	
Psiladiporites "faramensis"	angiosperm			
Psiladiporites "infragranulatus"	angiosperm			
Psiladiporites "annulatus"	angiosperm			
Psiladiporites sp. Varma & Rawat, 1963	angiosperm			
Psilamonocolpites "longiformis"	angiosperm			
Psilamonocolpites amazonicus Hoorn, 1993	angiosperm		Arecaceae	*Euterpe*
Psilamonocolpites medius (Van der Hammen, 1956) Van der Hammen and Garcia, 1966	angiosperm		Arecaceae	
Psilamonocolpites rinconii Duenas, 1986	angiosperm		Arecaceae	*Oenocarpus*
Psilaperiporites "juglands"	angiosperm			
Psilaperiporites minimus Regali et al., 1974	angiosperm	Chenopodiaceae/ Amaranthaceae	Amaranthaceae	
Psilastephanocolpites "janduforius"	angiosperm	Unknown Type 5		
Psilastephanocolporites "acalyphoides"	angiosperm		Euphorbiaceae	*Acalypha diversifolia*
Psilastephanocolporites "cedreloides"	angiosperm	*Cedrela*	Meliaceae	*Cedrela*
Psilastephanocolporites fissilis Leidelmeyer, 1966	angiosperm		Polygalaceae	
Psilastephanoporites "crassiannulatus"	angiosperm			
Psilastephanoporites "magnus"	angiosperm		Apocynaceae	
Psilastephanoporites "microcaribiensis"	angiosperm			
Psilastephanoporites "pareado"	angiosperm			
Psilastephanoporites "punctatus"	angiosperm			
Psilastephanoporites herngreenii Hoorn, 1993	angiosperm		Apocynaceae	

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Psilasyncolpites "recticolpatus"	angiosperm			
Psilasyncolporites "reticolpatus"	angiosperm			
Psilatricolpites CU490	angiosperm	Unknown Type 2		
Psilatricolpites sp. (Van der Hammen) Pierce, 1961	angiosperm			
Psilatricolporites "colpiconstrictus"	angiosperm			
Psilatricolporites "communis"	angiosperm			
Psilatricolporites "crassiexinatus"	angiosperm			
Psilatricolporites "faboides"	angiosperm			
Psilatricolporites "hornii"	angiosperm		Apocynaceae	
Psilatricolporites "poriperfectus"	angiosperm			
Psilatricolporites "rotund"	angiosperm			
Psilatricolporites "sphericus"	angiosperm			
Psilatricolporites "vest"	angiosperm			
Psilatricolporites "vestibulatus"	angiosperm			
Psilatricolporites costatus Dueñas, 1980	angiosperm	*Casearia*	Salicaceae	*Casearia*
Psilatricolporites sp. Van der Hammen ex. Pierce, 1961	angiosperm			
Psilatriporites "anilloides"	angiosperm			
Psilatriporites "lobatus"	angiosperm			
Psilatriporites "moraceoides"	angiosperm			
Psilatriporites "ulmoides"	angiosperm		Ulmaceae	
Psilatriporites "vestibulatum"	angiosperm			
Ranunculacidites operculatus (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm	*Alchornea*	Euphorbiaceae	*Alchornea*
Retibrevitricolporites "vestibulatum"	angiosperm			
Retidiporites "cordiaeformis"	angiosperm			
Retidiporites "vestibulatum"	angiosperm			
Retimonocolpites "colpimarginatus"	angiosperm			
Retimonocolpites "heteroretifossulatus"	angiosperm	*Manicaria*-type	Arecaceae	*Manicaria*
Retimonocolpites "palmatus"	angiosperm		Arecaceae	*Cryosophila*
Retipericolporites sp.	angiosperm			
Retipollenites "minutus"	angiosperm		Araceae	
Retistephanocolpites "brevicolpatus"	angiosperm		Rubiaceae	*Borreria*
Retistephanocolpites "hexalabiatus"	angiosperm			
Retistephanocolpites "octolabiatus"	angiosperm		Labiatae	
Retistephanocolporites "bombacoides"	angiosperm			
Retistephanocolporites "borrerioides"	angiosperm		Rubiaceae	*Borreria*
Retistephanocolporites "crassimuratus"	angiosperm			
Retistephanoporites aff. *crassiannulatus* Lorente, 1986	angiosperm		Malvaceae	
Retitrescolpites "amanoensis"	angiosperm		Phyllanthaceae	*Amanoa*
Retitrescolpites "amplibrochatus"	angiosperm			
Retitrescolpites "deformis"	angiosperm			
Retitrescolpites "homogeneus"	angiosperm			
Retitrescolpites "usualis"	angiosperm			

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Retitrescolpites? irregularis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Phyllanthaceae	*Amanoa*
Retitricolpites "generalis"	angiosperm			
Retitricolpites "pseudosimplex"	angiosperm			
Retitricolpites "spiraloides"	angiosperm	Unknown Type 14		
Retitricolpites simplex Gonzalez, 1967	angiosperm	*Sapium*	Euphorbiaceae	*Sapium*
Retitricolpites sp. (Van der Hammen) Pierce, 1961	angiosperm			
Retitricolporites "amplibrochatus"	angiosperm			
Retitricolporites "colpimarginatus"	angiosperm			
Retitricolporites "communis"	angiosperm	*Rourea*	Connaraceae	*Rourea*
Retitricolporites "crassiannulatus"	angiosperm		Rubiaceae	*Genipa americana*
Retitricolporites "hlongorate"	angiosperm			
Retitricolporites "minibrochatus"	angiosperm			
Retitricolporites "papilioniformis"	angiosperm		Faboideae	*Machaerium*
Retitricolporites "pluricolumellatus"	angiosperm	Unknown Type 7		
Retitricolporites "poricostatus"	angiosperm			
Retitricolporites "pseudoperculatus"	angiosperm			
Retitricolporites "simplibaculatus"	angiosperm			
Retitricolporites "spheroidalis"	angiosperm			
Retitricolporites "triangularis"	angiosperm			
Retitricolporites "zonoaperturatus"	angiosperm			
Retitricolporites "zonocolpatus"	angiosperm			
Retitricolporites CU456	angiosperm	*Cupania*	Sapindaceae	*Cupania*
Retitricolporites CU456-2	angiosperm	*Guazuma*	Byttneroideae	*Guazuma*
Retitricolporites CU57	angiosperm	Unknown Type 1		
Retitricolporites sp. Van der Hammen & Wymstra, 1964	angiosperm			
Retitriporites "erythrinoides"	angiosperm			
Retitriporites "heterobrochatus"	angiosperm			
Retitriporites "vestibulatum"	angiosperm		Rubiaceae	
Retitriporites aff. *poricostatus* Jaramillo and Dilcher, 2001	angiosperm			
Rhoipites "colpizonatus"	angiosperm			
Rhoipites "poricostatus"	angiosperm			
Rhoipites aff. *Cienagensis* (Dueñas, 1980) Barreda, 1997	angiosperm			
Rhoipites guianensis (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001	angiosperm		Malvaceae	
Rousea "cristatus"	angiosperm			
Rubiaceae (*Cosmibuena*) Ruiz & Pav.	angiosperm	*Cosmibuena*	Rubiaceae	*Cosmibuena*
Rubiaceae (*Faramea*) Aubl.	angiosperm	*Faramea*	Rubiaceae	*Faramea*
Rubiaceae (*Posoqueria*) Aubl.	angiosperm	*Posoqueria*	Rubiaceae	*Posoqueria*
Rubiaceae (Type 1)	angiosperm	Rubiaceae Type 1	Rubiaceae	
Rubiaceae (Type 2)	angiosperm	Rubiaceae Type 2	Rubiaceae	
Rubiopollis "muellerii"	angiosperm			

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Rutaceae (*Casimiroa*) La Llave & Lex.	angiosperm	*Casimiroa*	Rutaceae	*Casimiroa*
Sapindaceae (*Paullinia*) L.	angiosperm	*Paullinia*	Sapindaceae	*Paullinia*
Sapindaceae (*Serjania*) Mill.	angiosperm	*Serjania*	Sapindaceae	*Serjania*
Sapotaceae (cf. *Bumelia*) Sw.	angiosperm	cf. *Bumelia*	Sapotaceae	*Bumelia*
Scabraperiporites "nothofaguiformis"	angiosperm			
Scabrastephanoporites "apocynaceous"	angiosperm			
Siltaria "comunis"	angiosperm			
Siltaria dilcheri Silva-Caminha et al., 2010	angiosperm			
Stephanocolporites "lalongatus"	angiosperm			
Stephanoporites "scabratus"	angiosperm			
Striatopollis catatumbus (Gonzalez, 1967) Takahashi and Jux, 1989	angiosperm	*Crudia*	Caesalpinioideae	*Crudia*
Striatricolporites "burseriformis"	angiosperm	*Bursera*	Burseraceae	*Bursera simarouba*
Striatricolporites digitatus Jaramillo and Dilcher, 2001	angiosperm			
Striatricolporites melenae Dueñas, 1980	angiosperm		Anacardiaceae	
Striatricolporites tenuissimus Dueñas, 1980	angiosperm		Caesalpinioideae	*Crudia*
Symplocaceae (*Symplocos*) Jacq.	angiosperm	*Symplocos*	Symplocaceae	*Symplocos*
Syncolporites "paraisus"	angiosperm	*Matayba*	Sapindaceae	*Matayba*
Syncolporites "silvais"	angiosperm			
Syncolporites poricostatus van Hoeken Klinkenberg, 1966	angiosperm	*Eugenia/Myrcia*	Myrtaceae	*Eugenia-Myrcia*
Tetracolpites "rectangularis"	angiosperm			
Tetracolporites "guareaensis"	angiosperm	*Guarea*	Meliaceae	*Guarea*
Tetracolporites "meliaciformis"	angiosperm			
Tetracolporites "trichiliensis"	angiosperm		Meliaceae	*Trichilia*
Tetracolporites "vestibulatum"	angiosperm			
Tetracolporopollenites aff. *spongiosus* Jaramillo and Dilcher, 2001	angiosperm			
Tetracolporopollenites maculosus (Regali et al., 1974) Jaramillo and Dilcher, 2001	angiosperm		Sapotaceae	*Chrysophyllum*
Tetracolporopollenites transversalis (Dueñas, 1980) Jaramillo and Dilcher 2001	angiosperm		Sapotaceae	
Tiliaceae (*Mortoniodendron*) Standl. & Steyerm.	angiosperm	*Mortoniodendron*	Grewioideae	*Mortoniodendron*
Tricolpites "minutibacularis"	angiosperm			
Tricolpites "punctatus"	angiosperm	Unknown Type 3		
Tricolporites "annulatus"	angiosperm			
Tricolporites "caveatus"	angiosperm			
Tricolporites "colpidigitatus"	angiosperm			
Tricolporites "ericipitiformis"	angiosperm			
Tricolporites "megaporatus"	angiosperm			
Unknown 1	angiosperm	Unknown 1		
Unknown 2	angiosperm	Unknown 2		
Unknown 3	angiosperm	Unknown 3		
Unknown 4	angiosperm	Unknown 4		

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Unknown 5	angiosperm	Unknown 5		
Unknown 6	angiosperm	Unknown 6		
Unknown 7	angiosperm	Unknown 7		
Unknown 8	angiosperm	Unknown 8		
Unknown 9	angiosperm	Unknown 9		
Unknown 10	angiosperm	Unknown 10		
Unknown 11	angiosperm	Unknown 11		
Unknown 12	angiosperm	Unknown 12		
Unknown 13	angiosperm	Unknown 13		
Unknown 14	angiosperm	Unknown 14		
Unknown 15	angiosperm	Unknown 15		
Unknown 16	angiosperm	Unknown 16		
Unknown 17	angiosperm	Unknown 17		
Unknown 18	angiosperm	Unknown 18		
Unknown 19	angiosperm	Unknown 19		
Unknown 20	angiosperm	Unknown 20		
Unknown 21	angiosperm	Unknown 21		
Unknown 22	angiosperm	Unknown 22		
Unknown 23	angiosperm	Unknown 23		
Unknown 24	angiosperm	Unknown 24		
Unknown 25	angiosperm	Unknown 25		
Unknown 26	angiosperm	Unknown 26		
Unknown 27	angiosperm	Unknown 27		
Utricularia L.	angiosperm	*Utricularia*	Lentibulariaceae	*Utricularia*
Venezuelites "centroamericanus"	angiosperm			
Verbenaceae (*Aegiphila*) Jacq.	angiosperm	*Aegiphila*	Lamiaceae	Aegiphila
Verbenaceae *(Petrea)* L.	angiosperm	*Petrea*	Verbenaceae	Petrea
Verrutricolporites "desmodiensis"	angiosperm			
Verrutricolporites "faboides"	angiosperm			
Verrutricolporites "poricircularis"	angiosperm			
Verrutricolporites sp. Van der Hammen & Wymstra, 1964	angiosperm			
Vochysia type Aubl.	angiosperm		Vochysiaceae	Vochysia
Zonocostites "elongatus"	angiosperm			
Zonocostites ramonae Germeraad et al., 1968	angiosperm	*Rhizophora*	Rhizophoraceae	*Rhizophora*
Podocarpidites "globosus"	gymno-sperm	*Podocarpus*	Podocarpaceae	*Podocarpus*
Dinoflagellate	marine			
Foram lining	marine			
Anthocerotaceae	spore		Anthocerotaceae	
Apiculatasporites obscurus Jaramillo and Dilcher, 2001	spore	*Selaginella*	Selaginellaceae	*Selaginella*
Baculatisporites "circularis"	spore			
Baculatisporites "triangularis"	spore			
Camarozonoporites "crassus"	spore			

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Chomotriletes minor (Kedves, 1961) Pocock, 1970	spore			
Cicatricosisporites "bocatorensis"	spore			
Cingulatisporites "distafossulatus"	spore			
Cingulatisporites "gemmatus"	spore			
Cingulatisporites "pteriformis"	spore			
Cingulatisporites "rugulatus"	spore			
Cingulatisporites "verrutiformis"	spore			
Cingulatisporites psilatus Groot and Penny	spore			
Concavissimisporites "kyrtomatus"	spore			
Concavissimisporites fossulatus Duenas, 1980	spore			
Crassoretitriletes vanraadshooveni Germeraad et al., 1968	spore		Schizaeaceae	*Lygodium microphyllum*
Cyatheaceae (*Alsophila*) R. Br.	spore	*Alsophila*	Cyatheaceae	*Alsophila*
Cyatheaceae (*Cnemidaria*) C. Presl	spore	*Cnemidaria*	Cyatheaceae	*Cnemidaria*
Cyatheaceae (Type 1)	spore	Type 1	Cyatheaceae	
Cyatheaceae (Type 2)	spore	Type 2	Cyatheaceae	
Cyatheacidites annulatus Cookson, 1967	spore			
Cyathidites "typicus"	spore	*Cyathea*	Cyatheaceae	*Cyathea*
Leiotriletes adriennis (Potonie & Gelletich 1933) Krutzsch, 1959	spore			
Distaverrusporites "usmensis"	spore			
Dryopteridaceae (*Ctenitis*) (C. Chr.) C. Chr.	spore	*Ctenitis*	Dryopteridaceae	*Ctenitis*
Dryopteridaceae Type 1	spore	Dryopteridaceae Type 1	Dryopteridaceae	
Dryopteridaceae Type 2	spore	Dryopteridaceae Type 2	Dryopteridaceae	
Dryopteridaceae Type 3	spore	Dryopteridaceae Type 3	Dryopteridaceae	
Echinosporis sp. Krutzsch, 1967	spore			
Echinatisporis muelleri (Regali et al., 1974) Silva-Caminha et al., 2010	spore			
Echinomonoletes "amplimarginatus"	spore			
Echinomonoletes "bifurcatus"	spore			
Echinomonoletes "hirsutus"	spore			
Echinomonoletes "megaechinatus"	spore			
Echinomonoletes "sphericus"	spore			
Echitriletes "dasilviensis"	spore			
Echitriletes "densispinosus"	spore			
Echitriletes "minispinosus"	spore			
Echitriletes "minutuechinulatus"	spore			
Echitriletes "selaginelloides" type "baculanis"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "bifurcatus"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "echiplanatus"	spore		Selaginellaceae	
Echitriletes "selaginelloides" type "muelleri"	spore		Selaginellaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Echitriletes "selaginelloides" type "regularis"	spore		Selaginellaceae	
Echitriletes sp. Potonie, 1956	spore	*Selaginella*	Selaginellaceae	*Selaginella*
Fossutriletes "communis"	spore			
Fossutriletes "guapissimus"	spore			
Foveotriletes "arrugatus"	spore			
Foveotriletes "laterodepressus"	spore			
Foveotriletes "proximopsilatus"	spore	*Lycopodium*	Lycopodiaceae	*Lycopodium*
Foveotriletes "pseudoornatus"	spore			
Foveotriletes aff. *ornatus* Regali et al., 1974	spore			
Foveotriletes ornatus Regali et al., 1974	spore	Trilete fern spores Type 1 and 2		
Grammitisporites "verruminutus"	spore	*Grammitis*	Polypodiaceae	*Grammitis*
Kuylisporites "irregularis"	spore			
Kuylisporites "miniorodate"	spore			
Kuylisporites "multiorodate"	spore			
Kuylisporites waterbolki Potonié, 1956	spore		Cyatheaceae	*Hemitelia-Cnemidaria*
Laevigatosporites "magnus"	spore			
Laevigatosporites catanejensis Mullet et al., 1987	spore			
Laevigatosporites tibuensis (Van der Hammen, 1956a) Jaramillo and Dilcher, 2001	spore	Monolete fern spores Type 1 and 2		
Lycopodiaceae	spore	*Lycopodium* type 1	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 2	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 3	Lycopodiaceae	*Lycopodium*
Lycopodiaceae	spore	*Lycopodium* type 4	Lycopodiaceae	*Lycopodium*
Lycopodiumsporites "clavaelongatus"	spore		Lycopodiaceae	
Lycopodiumsporites "clavatus"	spore		Lycopodiaceae	
Lycopodiumsporites "morenoi"	spore		Lycopodiaceae	
Lycopodiumsporites "spinosus"	spore		Lycopodiaceae	
Lycopodiumsporites sp. Thiergart ex Delcourt & Sprumont, 1955	spore		Lycopodiaceae	
Matonisporites mulleri Playford, 1982	spore			
Monolete fern spore Type 1	spore	Monolete fern spore Type 1		
Monolete fern spore Type 2	spore	Monolete fern spore Type 2		
Monolete fern spore Type 3	spore	Monolete fern spore Type 3		
Monolete fern spore Type 4	spore	Monolete fern spore Type 4		
Monolete fern spore Type 5	spore	Monolete fern spore Type 5		
Nijssenosporites "pteridoides"	spore			
Nijssenosporites fossulatus Lorente, 1986	spore	*Pityrogramma*	Adianthaceae	*Pityrogramma*

(*continued*)

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Ophioglossaceae (*Ophioglossum*) L.	spore	*Ophioglossum*	Ophioglossaceae	*Ophioglossum*
Perinomonoletes "aciculiformis"	spore			
Perinomonoletes "microechinulatus"	spore			
Perinomonoletes "minispinosus"	spore			
Perinomonoletes "minutus"	spore			
Perinomonoletes "pseudoreticulatus"	spore			
Perinomonoletes "reticuloacicularis"	spore			
Perinomonoletes sp. Krutzsch, 1967	spore			
Planisporites sp. 2 Jaramillo and Dilcher, 2001	spore			
Polypodiaceoisporites pseudopsilatus Lorente, 1986	spore			
Polypodiaceoisporites "circularis"	spore			
Polypodiaceoisporites "reticulatus"	spore			
Polypodiaceoisporites fossulatus Jaramillo and Dilcher, 2001	spore			
Polypodiaceoisporites pseudopsilatus Lorente, 1986	spore		Pteridaceae	*Pteris*
Polypodiaceoisporites? fossulatus Jaramillo and Dilcher, 2001	spore	*Pteris*	Pteridaceae	*Pteris*
Polypodiisporites "microverrucate"	spore			
Polypodiisporites "planus"	spore			
Polypodiisporites "reniformis"	spore			
Polypodiisporites scabraproximatus Silva-Caminha et al., 2010	spore			
Polypodiisporites "verruplanatus"	spore			
Polypodiisporites aff. *echinatus* Jaramillo and Dilcher, 2001	spore			
Polypodiisporites aff. sp. 2 J & D Jaramillo and Dilcher, 2001	spore			
Polypodiisporites aff. *speciosus* Sah, 1967	spore	Monolete fern spore Type 3		
Polypodiisporites scabraproximatus Silva-Caminha et al., 2010	spore	Monolete fern spores Type 2		
Polypodiisporites usmensis (Van der Hammen, 1956a) Khan and Martin, 1972	spore		Blechnaceae	*Stenochlaena palustris*
Polypodiisporites? planus Silva-Caminha et al., 2010	spore			
Psilatriletes "brevilaesuratus"	spore	*Antrophyum*	Pteridaceae	*Antrophyum*
Psilatriletes "camerata"	spore			
Psilatriletes "crassitriangulatus"	spore			
Psilatriletes "enormis"	spore	*Lygodium*	Lygodiaceae	*Lygodium*
Psilatriletes "minor"	spore			
Psilatriletes < 25 µm	spore			
Psilatriletes > 50 µm	spore			
Psilatriletes 25–50 µm	spore	*Cyathea*	Cyatheaceae	*Cyathea*
Psilatriletes lobatus Hoorn, 1994	spore			
Psilatriletes peruanus Hoorn, 1994	spore		Pteridaceae	*Jamesonia*
Pteridaceae (Type 1)	spore	Pteridaceae Type 1	Pteridaceae	

TABLE 4. (*continued*)

Taxon	Category	Graham taxon name	Family	Genus
Pteridaceae (Type 2)	spore	Pteridaceae Type 2	Pteridaceae	
Pteridaceae (Type 3)	spore	Pteridaceae Type 3	Pteridaceae	
Pteridaceae (Type 4)	spore	Pteridaceae Type 4	Pteridaceae	
Pteridaceae (Type 5)	spore	Pteridaceae Type 5	Pteridaceae	
Retitriletes "perforatus"	spore			
Retitriletes sommeri Regali et al., 1974	spore	Trilete fern spores Type 3	Lycopodiaecae	
Rugulatisporites "irregularis"	spore			
Rugulatisporites "minutus"	spore			
Scabramonoletes "elongatus"	spore			
Scabratriletes "complicatus"	spore			
Schizaea "mosquitensis"	spore			
Selaginellasporites "cingulatus"	spore		Selaginellaceae	
Selaginellasporites "crestatus"	spore		Selaginellaceae	
Selaginellasporites "psilatus"	spore		Selaginellaceae	
Selaginellasporites "variechinatus"	spore		Selaginellaceae	
Striatomonoletes "inciertus"	spore			
Striatriletes "saccolomicites"	spore			
Trilete fern spore Type 1	spore	Trilete fern spore Type 1		
Trilete fern spore Type 2	spore	Trilete fern spore Type 2		
Undulatisporites "undulapolus"	spore			
Verrucatotriletes etayoi Duenas, 1980	spore			
Verrucatotriletes sp. van Hoeken-Klinkenberg, 1964	spore			
Verrutriletes "bullatus"	spore			
Verrutriletes "densiverrucatus"	spore			
Verrutriletes "magnoviruelensis"	spore			
Verrutriletes "perforatus"	spore			
Verrutriletes "uniformis"	spore			
Verrutriletes "variverrucatus"	spore			
Verrutriletes sp. Pierce, 1961	spore	Trilete fern spores Type 4		
Baculatriletes "palmiformis"	spore			
Echimonoletes "panamensis"	spore	*Danaea*	Marattiaceae	*Danaea*

Samples were divided into three groups (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma) because, as mentioned previously, they represent three major periods in the geological evolution of the isthmus history. All comparisons are the result of two-sided *t*-tests to evaluate the equality of means in two unpaired samples. Probability (*P*) is reported for each test, along with degrees of freedom (*df*) calculated using the Welch modification to account for different variances in the groups being compared. All analyses were done using R Project for Statistical Computing (R Development Core Team, 2012) and the package "vegan" (Oksanen et al., 2010). All R codes used here are presented in Appendix 3. Samples with less than 80 grains (excluding fungi) were excluded from most of the analyses.

RESULTS

OVERALL PATTERN

A total of 27,910 grains (pollen/spores), yielding 496 morphotypes in 282 samples, were registered (Tables 4, 5, Supplementary Appendix, Appendix 2). Angiosperm abundance per sample did not change substantially across the 19.5–3.5 Ma interval (40% in the 19.5–10 Ma interval, 36% in the 10–3.5 Ma interval, $P = 0.2$, $df = 109$), and slightly decreased in the last 3.5 Ma (26%), although the difference is not significant ($P = 0.07$, $df = 17$) (Fig. 3). Ferns represent 59% of the abundance per sample in the 19.5–10 Ma interval, and 62% in the 10–3.5 Ma interval ($P = 0.3$, $df = 108$), increasing slightly in the last 3.5 Ma (73%, $P = 0.07$, $df = 17$), although the difference is not significant (Fig. 3).

Biogeographic affinities. The biogeographic affinity of each individual extant tree and shrub in the Barro Colorado Island (BCI) 50-ha vegetation plot is dominated by Gondwana-Amazonian families: 68% of individuals are Gondwana-Amazonian, 20.5% are Gondwana-northern Andean, 3.2% are Gondwana-southern Andean, and only 6.1% are Laurasian (2.2% are unassigned to families) (Fig. 4, Appendix 1). We analyzed the biogeographic affinities of the entire fossil dataset (496 taxa) but only in samples with counts larger than 80 grains ($N = 124$). The mean of Gondwana-Amazonian individuals in a sample is 27% (SD = 16.9); Gondwana-northern Andean, 1% (SD = 1.7); Gondwana-southern Andean, 0.5% (SD = 1.3); and Laurasian-centered, 1.8% (SD = 0.2) (Fig. 4, Table 5). There was still a large proportion of individuals excluded from this calculation (69%, SD = 16.6), because either the family does not have a distinct biogeographic origin (23 taxa) or the family that the individual belongs to is still unknown (315 taxa). Does this proportion change when time slots are analyzed independently? Gondwana-Amazonian taxa are significantly more abundant prior to 3.5 Ma (> 3.5 Ma: 28%; < 3.5 Ma: 17%; $P = 0.03$, $df = 12$). Conversely, Laurasian taxa (> 3.5 Ma: 1.7%; < 3.5 Ma: 2.5%) and northern Andean taxa (> 3.5 Ma: 1%; < 3.5 Ma: 1.7%) are slightly less abundant prior to 3.5 Ma, although these differences are not significant ($P = 0.2$, $df = 12$ and $P = 0.1$, $df = 16$, respectively) (Fig. 4). Amazonian taxa are slightly more abundant prior to 10 Ma, compared to the 10–3.5 Ma interval, although the difference is not significant (19.5–10 Ma: 31.8%; 10–3.5 Ma: 24.6%; $P = 0.02$, $df = 108$), while Laurasian taxa are significantly more abundant in the 10–3.5 Ma interval compared to older strata (10–3.5 Ma: 2.8%; 19.5–10 Ma: 0.8%; $P = 0.001$, $df = 92$); the same pattern is depicted by northern Andean taxa (10–3.5 Ma: 1.9%; 19.5–10 Ma: 0.3%; $P = 0.001$, $df = 63$) (Fig. 4).

Extant species on BCI are dominated by South American families: 66.4% of species are Gondwana-Amazonian, 13.1% are Gondwana-northern Andean, and 4.8%, Gondwana-southern Andean, while only 10.9% are Laurasian (4.4% are unassigned families) (Fig. 5, Appendix 1). The biogeographic affinity of each fossil taxon is very similar to the pattern described for extant plants: the Gondwana-Amazonian mean is 26.7% (SD

TABLE 5. Summary table. The following values correspond to pollen/spore grains and species counted in each sample, and abundances (given as percentages) of species grouped by both biogeographic and ecological categories. Samples with counts of < 80 grains are included here but were not considered for the biogeographic and ecological analyses.

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Swan Cay	1.285	34	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	1.810	81	30	29.8	0.14	0.02	0.04	0.06	0.74	0.20	0.20	0.15	0.05	0.00	0.00	0.05	0.01	0.72
Bocas del Toro	Nancy Point	1.820	57	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.000	123	17	15.15	0.12	0.02	0.00	0.02	0.84	0.04	0.02	0.02	0.00	0.00	0.00	0.08	0.00	0.88
Bocas del Toro	Escudo Veraguas	2.051	111	31	24.8	0.44	0.04	0.00	0.04	0.49	0.26	0.23	0.17	0.04	0.00	0.00	0.29	0.01	0.43
Bocas del Toro	Escudo Veraguas	2.052	78	31	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	2.053	76	27	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	2.054	158	36	24.56	0.32	0.01	0.01	0.01	0.64	0.29	0.27	0.20	0.08	0.01	0.00	0.19	0.00	0.49
Bocas del Toro	Escudo Veraguas	2.055	326	47	26.85	0.23	0.02	0.02	0.05	0.68	0.19	0.16	0.12	0.04	0.01	0.00	0.12	0.00	0.67
Bocas del Toro	unnamed	2.300	45	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.400	298	31	17.79	0.05	0.01	0.01	0.05	0.88	0.18	0.16	0.14	0.00	0.01	0.00	0.03	0.01	0.77
Bocas del Toro	unnamed	2.500	21	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	2.651	297	46	26.44	0.06	0.02	0.01	0.04	0.86	0.24	0.23	0.23	0.01	0.01	0.00	0.04	0.00	0.68
Bocas del Toro	unnamed	2.652	141	20	15.92	0.08	0.01	0.00	0.01	0.91	0.04	0.02	0.02	0.00	0.00	0.00	0.06	0.00	0.90
Bocas del Toro	unnamed	2.653	105	12	10.75	0.02	0.00	0.00	0.00	0.98	0.03	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.96
Bocas del Toro	Escudo de Veraguas	2.751	22	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.752	105	18	15.63	0.36	0.01	0.00	0.01	0.62	0.06	0.04	0.01	0.01	0.00	0.00	0.33	0.00	0.61
Bocas del Toro	Escudo de Veraguas	2.753	14	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.754	297	40	19.41	0.04	0.01	0.00	0.00	0.95	0.18	0.15	0.15	0.00	0.00	0.00	0.01	0.00	0.79
Bocas del Toro	Escudo de Veraguas	2.755	31	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.756	39	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.757	13	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	2.758	26	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	3.450	72	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	3.451	38	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(continued)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Escudo de Veraguas	3.551	52	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.551	38	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.551	79	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	3.551	68	29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo Veraguas	3.551	61	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	70	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	32	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	37	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	65	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Escudo de Veraguas	3.552	308	38	21.82	0.16	0.02	0.01	0.00	0.81	0.17	0.14	0.13	0.00	0.00	0.00	0.12	0.00	0.71
Bocas del Toro	Escudo de Veraguas	3.552	52	24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	3.552	67	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.552	31	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.552	77	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	94	28	25.95	0.23	0.05	0.00	0.02	0.69	0.16	0.12	0.10	0.00	0.00	0.00	0.18	0.00	0.65
Bocas del Toro	Cayo Agua	3.553	71	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	70	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	9	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	111	27	24.29	0.23	0.07	0.01	0.07	0.61	0.29	0.27	0.16	0.05	0.00	0.00	0.09	0.00	0.59
Bocas del Toro	Cayo Agua	3.553	264	48	23.37	0.41	0.03	0.01	0.01	0.54	0.22	0.21	0.19	0.01	0.00	0.02	0.19	0.00	0.56
Bocas del Toro	Cayo Agua	3.553	101	25	21.74	0.06	0.01	0.00	0.06	0.87	0.16	0.11	0.14	0.01	0.00	0.01	0.02	0.00	0.75
Bocas del Toro	Cayo Agua	3.553	32	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	42	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	3.553	46	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	3.554	109	30	24.69	0.16	0.05	0.00	0.06	0.74	0.38	0.37	0.32	0.06	0.01	0.00	0.06	0.00	0.53
Bocas del Toro	unnamed	3.554	5	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Bocas del Toro	unnamed	3554	279	35	21.08	0.08	0.00	0.00	0.03	0.89	0.23	0.19	0.16	0.00	0.01	0.00	0.00	0.00	0.75
Bocas del Toro	unnamed	3554	171	37	26.32	0.07	0.03	0.01	0.02	0.87	0.19	0.14	0.13	0.02	0.01	0.00	0.02	0.00	0.77
Bocas del Toro	Shark Hole Point	4000	206	40	25.4	0.20	0.01	0.00	0.01	0.78	0.22	0.19	0.14	0.04	0.01	0.00	0.08	0.00	0.69
Bocas del Toro	Cayo Agua	4250	196	34	22.45	0.35	0.03	0.00	0.01	0.61	0.18	0.17	0.11	0.05	0.01	0.00	0.25	0.00	0.56
Bocas del Toro	Cayo Agua	4250	41	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4250	6	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4250	11	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	7	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	23	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	23	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	45	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	35	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	35	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	70	25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	22	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	36	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4251	17	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4252	67	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4252	92	28	26.59	0.18	0.05	0.00	0.10	0.66	0.21	0.21	0.21	0.02	0.00	0.02	0.07	0.00	0.63
Bocas del Toro	Cayo Agua	4252	140	32	25.59	0.21	0.03	0.02	0.04	0.69	0.24	0.22	0.20	0.03	0.01	0.00	0.16	0.00	0.37
Bocas del Toro	Cayo Agua	4252	85	23	22.29	0.44	0.08	0.02	0.02	0.44	0.20	0.20	0.19	0.02	0.00	0.00	0.35	0.01	0.40
Bocas del Toro	Cayo Agua	4252	76	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4252	37	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4252	149	45	31.05	0.03	0.00	0.01	0.00	0.97	0.03	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.98
Bocas del Toro	Cayo Agua	4252	26	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4252	121	43	80.67	0.21	0.02	0.01	0.05	0.70	0.31	0.28	0.23	0.02	0.00	0.00	0.11	0.00	0.56
Bocas del Toro	Cayo Agua	4252	7	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4253	21	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4253	174	29	20.48	0.04	0.03	0.01	0.01	0.94	0.19	0.17	0.17	0.00	0.00	0.02	0.02	0.00	0.76
Bocas del Toro	Cayo Agua	4253	88	20	19.14	0.11	0.01	0.00	0.00	0.88	0.14	0.11	0.09	0.00	0.00	0.00	0.07	0.00	0.80
Bocas del Toro	Cayo Agua	4253	148	21	15.7	0.06	0.03	0.00	0.01	0.9	0.30	0.27	0.26	0.01	0.00	0.01	0.04	0.00	0.63
Bocas del Toro	Cayo Agua	4253	95	24	22.23	0.06	0.00	0.01	0.01	0.88	0.16	0.18	0.20	0.01	0.00	0.00	0.04	0.01	0.73

(continued)

TABLE 5. *(continued)*

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Bocas del Toro	Cayo Agua	4.253	48	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	15	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	49	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	57	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Cayo Agua	4.253	34	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	unnamed	4.254	33	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.400	25	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.610	6	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Shark Hole Point	4.620	164	36	27.52	0.15	0.01	0.00	0.02	0.82	0.13	0.14	0.13	0.01	0.00	0.01	0.05	0.00	0.76
Bocas del Toro	Shark Hole Point	4.630	99	26	23.8	0.07	0.01	0.00	0.03	0.89	0.15	0.15	0.15	0.01	0.00	0.00	0.01	0.00	0.81
Bocas del Toro	Nancy Point	5.650	132	25	19.57	0.32	0.02	0.01	0.00	0.66	0.20	0.19	0.14	0.05	0.01	0.00	0.23	0.00	0.55
Panama Central	Gatun	6.000	114	25	21.51	0.43	0.10	0.01	0.04	0.43	0.25	0.22	0.16	0.04	0.00	0.00	0.22	0.01	0.50
Panama Central	Chagres	6.010	156	29	21.14	0.13	0.01	0.00	0.02	0.83	0.36	0.31	0.26	0.05	0.01	0.00	0.03	0.00	0.60
Panama Central	Chagres	6.020	106	22	20.04	0.06	0.01	0.01	0.00	0.92	0.12	0.08	0.08	0.00	0.00	0.00	0.01	0.00	0.86
Bocas del Toro	Nancy Point	6.051	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.052	22	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.307	16	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bocas del Toro	Nancy Point	6.400	54	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	6.400	16	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	6.410	40	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.910	13	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Pucro	6.950	18	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.950	9	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Chucunaque	6.950	14	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	12	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	6.951	82	22	21.73	0.23	0.01	0.00	0.01	0.76	0.02	0.02	0.02	0.00	0.00	0.00	0.15	0.00	0.83

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Gatun	8.400	163	25	21.35	0.30	0.03	0.09	0.03	0.55	0.32	0.32	0.10	0.00	0.09	0.08	0.04	0.00	0.43
Panama Central	Gatun	8.407	182	25	17.32	0.46	0.02	0.07	0.02	0.43	0.29	0.29	0.03	0.00	0.07	0.22	0.03	0.00	0.36
Panama Central	Gatun	8.412	240	88	42.74	0.24	0.05	0.08	0.04	0.59	0.26	0.26	0.10	0.03	0.04	0.08	0.04	0.00	0.55
Panama Central	Gatun	8.418	199	15	9.881	0.90	0.00	0.01	0.01	0.08	0.07	0.05	0.02	0.02	0.00	0.04	0.82	0.00	0.06
Panama Central	Gatun	8.472	176	23	19.86	0.30	0.00	0.03	0.04	0.63	0.20	0.23	0.16	0.00	0.00	0.19	0.11	0.09	0.37
Panama Central	Gatun	8.473	179	21	16.34	0.35	0.01	0.00	0.00	0.64	0.14	0.10	0.09	0.01	0.01	0.30	0.11	0.08	0.36
Panama Central	Gatun	8.474	182	16	15.07	0.37	0.02	0.00	0.05	0.55	0.16	0.15	0.14	0.00	0.00	0.31	0.10	0.08	0.30
Panama Central	Gatun	8.563	184	18	15.18	0.33	0.02	0.00	0.03	0.63	0.08	0.11	0.08	0.00	0.00	0.25	0.09	0.00	0.55
Panama Central	Gatun	8.596	179	14	12.45	0.16	0.02	0.02	0.04	0.77	0.11	0.16	0.14	0.01	0.00	0.20	0.08	0.00	0.56
Panama Central	Gatun	8.610	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.620	13	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.630	23	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.640	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.650	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.660	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.670	49	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.726	265	21	14.36	0.19	0.00	0.00	0.01	0.80	0.23	0.23	0.17	0.01	0.00	0.00	0.08	0.00	0.67
Panama Central	Gatun	8.753	156	25	19.16	0.14	0.00	0.00	0.01	0.85	0.17	0.15	0.08	0.00	0.00	0.01	0.01	0.00	0.81
Panama Central	Gatun	8.754	287	35	21.85	0.25	0.00	0.03	0.03	0.68	0.09	0.06	0.01	0.00	0.00	0.00	0.09	0.00	0.81
Panama Central	Gatun	8.754	69	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	8.770	363	58	25.52	0.27	0.01	0.01	0.01	0.69	0.31	0.26	0.16	0.02	0.01	0.00	0.02	0.00	0.65
Panama Central	Gatun	8.773	746	66	21.39	0.34	0.00	0.00	0.04	0.61	0.23	0.22	0.07	0.01	0.00	0.00	0.08	0.00	0.67
Panama Central	Gatun	9.398	41	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.401	11	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.402	24	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.412	219	22	14.28	0.32	0.00	0.00	0.00	0.67	0.09	0.07	0.06	0.00	0.00	0.00	0.24	0.00	0.67
Panama Central	Gatun	9.424	58	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Panama Central	Gatun	9.432	83	24	23.56	0.05	0.04	0.00	0.10	0.82	0.24	0.25	0.23	0.02	0.00	0.01	0.00	0.00	0.71
Panama Central	Gatun	9.464	63	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.500	34	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.519	37	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.552	50	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.589	137	29	21.78	0.09	0.00	0.00	0.05	0.86	0.07	0.09	0.06	0.03	0.00	0.01	0.02	0.00	0.86
Panama Central	Gatun	9.737	171	36	26.73	0.25	0.01	0.01	0.04	0.70	0.44	0.32	0.29	0.05	0.00	0.00	0.04	0.00	0.48
Panama Central	Gatun	9.932	207	37	22.78	0.15	0.03	0.01	0.02	0.79	0.17	0.14	0.10	0.02	0.00	0.00	0.02	0.00	0.79
Panama Central	Gatun	9.932	17	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	9.932	129	26	21.23	0.15	0.00	0.00	0.05	0.80	0.23	0.22	0.20	0.02	0.00	0.00	0.05	0.00	0.69
Panama Central	Gatun	10.143	323	43	21.97	0.25	0.02	0.01	0.05	0.67	0.29	0.27	0.22	0.03	0.00	0.01	0.14	0.00	0.55
Darien	Tuira	10.151	50	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.152	44	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.153	49	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.154	30	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.155	47	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.156	23	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	10.157	19	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	10.874	91	19	18.09	0.04	0.01	0.00	0.09	0.86	0.46	0.47	0.48	0.02	0.00	0.00	0.00	0.00	0.49
Panama Central	Gatun	10.877	299	29	18.93	0.24	0.00	0.00	0.01	0.75	0.10	0.09	0.03	0.00	0.00	0.00	0.03	0.00	0.86
Panama Central	Gatun	10.878	129	26	20.73	0.05	0.00	0.00	0.02	0.93	0.16	0.13	0.11	0.00	0.00	0.00	0.00	0.00	0.84
Panama Central	Gatun	10.881	268	32	19.4	0.08	0.01	0.00	0.01	0.90	0.07	0.05	0.03	0.00	0.00	0.00	0.00	0.00	0.93
Panama Central	Gatun	10.883	51	15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Gatun	11.553	185	43	29.46	0.22	0.04	0.00	0.02	0.72	0.29	0.26	0.20	0.05	0.02	0.02	0.06	0.01	0.60
Panama Central	Gatun	11.674	139	29	22.79	0.08	0.01	0.00	0.06	0.85	0.20	0.18	0.17	0.03	0.00	0.00	0.00	0.00	0.78
Darien	Tuira	12.601	12	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.602	13	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.603	15	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Darien	Tuira	12.604	7	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	18.834	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	18.915	86	8	8	0.65	0.00	0.00	0.00	0.35	0.13	0.09	0.03	0.35	0.00	0.00	0.07	0.00	0.45
Panama Central	Cucaracha	18.925	6	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(continued)

TABLE 5. *(continued)*

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Culebra	18.928	82	11	10.95	0.43	0.00	0.00	0.00	0.57	0.20	0.16	0.06	0.04	0.01	0.00	0.10	0.00	0.66
Panama Central	Culebra	18.931	86	14	13.65	0.53	0.00	0.00	0.01	0.45	0.38	0.38	0.27	0.13	0.00	0.00	0.10	0.00	0.37
Panama Central	Culebra	18.935	94	13	12.66	0.43	0.00	0.00	0.00	0.57	0.37	0.35	0.21	0.13	0.00	0.00	0.05	0.00	0.45
Panama Central	Culebra	18.948	182	38	28.08	0.35	0.01	0.00	0.03	0.62	0.35	0.35	0.15	0.04	0.01	0.02	0.03	0.00	0.58
Panama Central	Culebra	18.953	182	19	13.79	0.41	0.00	0.00	0.01	0.59	0.37	0.32	0.18	0.02	0.00	0.00	0.02	0.00	0.61
Panama Central	Culebra	18.954	181	32	26.04	0.33	0.00	0.02	0.04	0.61	0.40	0.37	0.20	0.06	0.00	0.00	0.06	0.00	0.48
Panama Central	Culebra	18.961	185	25	19.62	0.36	0.01	0.01	0.01	0.63	0.32	0.24	0.18	0.05	0.00	0.02	0.09	0.00	0.53
Panama Central	Culebra	18.962	162	17	15.04	0.27	0.00	0.00	0.00	0.73	0.41	0.33	0.23	0.04	0.01	0.00	0.04	0.00	0.51
Panama Central	Culebra	18.962	187	12	10.64	0.29	0.00	0.00	0.00	0.71	0.25	0.21	0.16	0.11	0.00	0.00	0.04	0.00	0.59
Panama Central	Culebra	18.962	180	13	11.77	0.27	0.00	0.00	0.00	0.73	0.49	0.40	0.31	0.07	0.00	0.00	0.12	0.00	0.33
Panama Central	Cucaracha	18.974	323	9	5.957	0.76	0.00	0.00	0.00	0.24	0.03	0.03	0.01	0.00	0.00	0.00	0.21	0.00	0.00	0.76
Panama Central	Cucaracha	18.974	223	15	10.53	0.48	0.00	0.00	0.00	0.52	0.04	0.04	0.02	0.00	0.00	0.07	0.01	0.00	0.89
Panama Central	Cucaracha	18.981	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.061	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.086	299	16	10.89	0.54	0.00	0.00	0.00	0.46	0.14	0.14	0.10	0.00	0.00	0.10	0.00	0.00	0.77
Panama Central	Cucaracha	19.100	10	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.143	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.173	298	22	13.91	0.35	0.00	0.00	0.00	0.65	0.16	0.16	0.14	0.00	0.01	0.03	0.00	0.00	0.81
Panama Central	Cucaracha	19.175	167	18	13.46	0.44	0.00	0.00	0.00	0.56	0.21	0.21	0.20	0.00	0.01	0.07	0.00	0.00	0.78
Panama Central	Cucaracha	19.196	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.201	179	26	17.63	0.22	0.00	0.00	0.00	0.78	0.25	0.23	0.21	0.00	0.00	0.08	0.02	0.00	0.66
Panama Central	Cucaracha	19.203	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.210	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.215	117	21	18.01	0.30	0.00	0.00	0.01	0.69	0.27	0.26	0.23	0.01	0.00	0.02	0.00	0.00	0.70
Panama Central	Cucaracha	19.230	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.241	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.241	172	19	15.12	0.19	0.01	0.00	0.01	0.80	0.32	0.29	0.27	0.01	0.00	0.05	0.00	0.00	0.63

Panama Central	Cucaracha	19.251	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.254	108	20	17.92	0.27	0.00	0.00	0.00	0.73	0.28	0.24	0.23	0.01	0.00	0.01	0.00	0.00	0.72
Panama Central	Cucaracha	19.262	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.264	326	10	8.192	0.30	0.00	0.00	0.00	0.70	0.15	0.15	0.02	0.00	0.00	0.04	0.00	0.00	0.80
Panama Central	Culebra	19.268	101	23	20.33	0.22	0.00	0.00	0.00	0.78	0.26	0.13	0.12	0.02	0.01	0.04	0.00	0.00	0.69
Panama Central	Cucaracha	19.269	321	8	5.935	0.31	0.00	0.00	0.00	0.69	0.13	0.13	0.00	0.00	0.00	0.14	0.00	0.00	0.74
Panama Central	Cucaracha	19.278	132	20	16.84	0.09	0.00	0.00	0.00	0.91	0.21	0.19	0.20	0.01	0.01	0.05	0.00	0.00	0.73
Panama Central	Culebra	19.281	54	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Cucaracha	19.290	140	17	13.38	0.11	0.01	0.00	0.00	0.89	0.34	0.34	0.34	0.00	0.01	0.19	0.01	0.00	0.54
Panama Central	Culebra	19.294	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.308	171	16	12.39	0.37	0.00	0.00	0.01	0.61	0.29	0.30	0.30	0.01	0.00	0.22	0.11	0.00	0.58
Panama Central	Cucaracha	19.311	133	19	16.26	0.11	0.00	0.00	0.00	0.89	0.26	0.21	0.20	0.00	0.02	0.08	0.00	0.00	0.68
Panama Central	Culebra	19.316	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.321	238	19	15.01	0.25	0.00	0.00	0.00	0.75	0.11	0.11	0.11	0.00	0.00	0.16	0.03	0.00	0.71
Panama Central	Culebra	19.327	102	17	15.97	0.68	0.00	0.00	0.00	0.32	0.14	0.14	0.08	0.00	0.01	0.02	0.07	0.00	0.76
Panama Central	Culebra	19.334	73	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.347	53	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.374	55	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.381	270	22	13.52	0.19	0.00	0.00	0.00	0.80	0.14	0.15	0.14	0.00	0.00	0.23	0.00	0.00	0.63
Panama Central	Culebra	19.385	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.398	150	19	16.49	0.45	0.00	0.00	0.01	0.55	0.29	0.15	0.09	0.01	0.00	0.03	0.00	0.00	0.67
Panama Central	Culebra	19.407	177	21	17.58	0.44	0.00	0.00	0.00	0.56	0.21	0.21	0.15	0.00	0.00	0.02	0.01	0.00	0.76
Panama Central	Culebra	19.409	281	22	14.09	0.37	0.00	0.00	0.00	0.63	0.11	0.10	0.08	0.01	0.00	0.10	0.10	0.01	0.70
Panama Central	Culebra	19.414	8	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Panama Central	Culebra	19.416	198	21	15.79	0.39	0.00	0.00	0.01	0.61	0.28	0.25	0.22	0.00	0.00	0.01	0.00	0.00	0.71
Panama Central	Culebra	19.425	277	25	18.11	0.51	0.00	0.00	0.00	0.49	0.28	0.25	0.20	0.00	0.00	0.03	0.00	0.00	0.69
Panama Central	Culebra	19.433	251	21	15.61	0.34	0.00	0.00	0.02	0.65	0.28	0.25	0.20	0.00	0.01	0.04	0.00	0.00	0.66
Panama Central	Culebra	19.434	313	29	20	0.47	0.00	0.00	0.02	0.51	0.26	0.27	0.23	0.00	0.00	0.01	0.01	0.00	0.70
Panama Central	Culebra	19.444	303	27	15.52	0.33	0.00	0.00	0.00	0.67	0.45	0.46	0.38	0.00	0.00	0.03	0.00	0.00	0.51
Panama Central	Culebra	19.454	285	22	14.35	0.34	0.00	0.00	0.02	0.64	0.33	0.35	0.32	0.00	0.00	0.03	0.00	0.00	0.61
Panama Central	Culebra	19.462	301	23	13.44	0.36	0.00	0.00	0.00	0.64	0.11	0.11	0.11	0.00	0.00	0.10	0.03	0.01	0.77
Panama Central	Culebra	19.462	194	17	11.73	0.28	0.00	0.00	0.01	0.71	0.30	0.30	0.26	0.01	0.00	0.01	0.00	0.00	0.68

(continued)

TABLE 5. (*continued*)

Area	Formation	Sample age (Ma)	N[1]	S	S(80)	AZ (%)	NAN (%)	SAN (%)	LA (%)	U (%)	TRFO (%)	PMF (%)	MF (%)	TDFO (%)	SV (%)	FW (%)	MG (%)	MR (%)	UK (%)
Panama Central	Culebra	19.470	299	20	14.12	0.22	0.00	0.00	0.00	0.77	0.43	0.41	0.39	0.02	0.00	0.06	0.00	0.00	0.50
Panama Central	Culebra	19.478	313	18	12.52	0.27	0.00	0.00	0.01	0.72	0.35	0.36	0.33	0.00	0.01	0.02	0.00	0.00	0.62
Panama Central	Cucaracha	19.479	100	12	11.67	0.34	0.00	0.02	0.01	0.63	0.18	0.19	0.13	0.00	0.00	0.00	0.17	0.00	0.64
Panama Central	Cucaracha	19.480	100	6	5.76	0.21	0.00	0.00	0.00	0.79	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.00	0.83
Panama Central	Cucaracha	19.480	100	4	3.962	0.08	0.00	0.00	0.00	0.92	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.98
Panama Central	Cucaracha	19.481	100	8	7.523	0.18	0.02	0.00	0.01	0.79	0.04	0.04	0.01	0.00	0.00	0.00	0.09	0.00	0.87
Panama Central	Culebra	19.485	310	17	10.87	0.32	0.00	0.00	0.01	0.67	0.40	0.41	0.36	0.01	0.00	0.02	0.00	0.00	0.57
Panama Central	Culebra	19.493	289	19	12.65	0.26	0.00	0.00	0.00	0.74	0.50	0.49	0.46	0.00	0.00	0.03	0.01	0.00	0.46
Panama Central	Cucaracha	19.525	100	9	8.193	0.17	0.00	0.00	0.00	0.83	0.03	0.03	0.01	0.00	0.00	0.02	0.07	0.00	0.89
Panama Central	Cucaracha	19.527	100	5	4.993	0.26	0.00	0.00	0.00	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.87
Panama Central	Cucaracha	19.528	97	5	4.825	0.74	0.00	0.00	0.00	0.26	0.01	0.01	0.00	0.00	0.00	0.00	0.62	0.00	0.37

[1] Abbreviations: *N* = number of individuals (pollen/spore grains) counted per sample; S = number of species; S(80) = rarefied number of species at a cutoff of 80 grains; AZ = Gondwana-Amazonian; NAN = Gondwana-northern Andean; SAN = Gondwana-southern Andean; LA = Laurasian; U = Unassigned; TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community; UK = unknown.

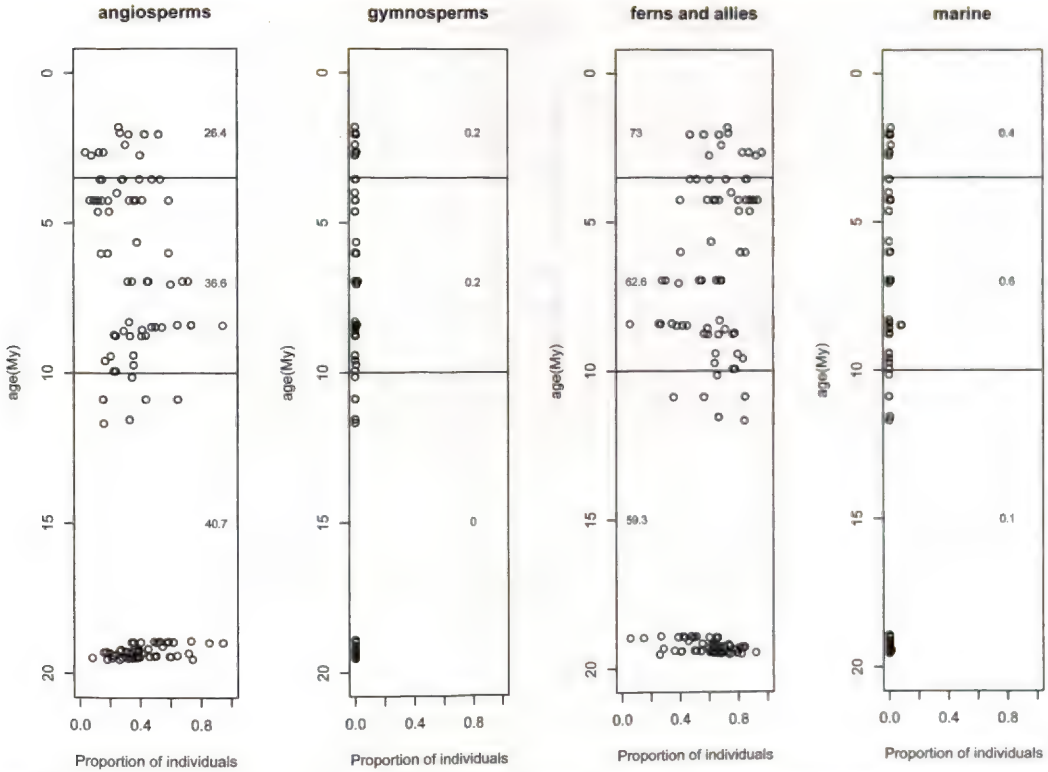

FIGURE 3. Proportion of the abundance of individuals per sample of the main groups of palynomorphs found in this study, including angiosperms, gymnosperms, fern spores and allies, and marine palynomorphs. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side.

= 1); Gondwana-northern Andean, 3.8% (SD = 4.3); Gondwana-southern Andean, 1.5% (SD = 2.4); and Laurasian, 4.2% (SD = 3.6) (Fig. 5, Table 5). However, 63% (SD = 11) of species are still unassigned to families because either the family does not have a distinct biogeographic origin (23 taxa) or the natural affinity of the species is still unknown (315 taxa). Does this proportion change when time slots are analyzed independently? Amazonian taxa are significantly more abundant prior to 3.5 Ma (> 3.5 Ma: 27.6%; < 3.5 Ma: 18.7%; $P = 0.001$, $df = 17$), Laurasian taxa do not change (> 3.5 Ma: 4.1%; < 3.5 Ma: 5.7%; $P = 0.2$, $df = 11$), and northern Andean taxa are significantly more abundant in the last 3.5 My (> 3.5 Ma: 3.6%; < 3.5 Ma: 6.4%; $P = 0.01$, $df = 14$). Amazonian taxa are more abundant > 10 Ma compared to the 10–3.5 Ma interval (19.5–10 Ma: 30.7%; 10–3.5 Ma: 24.2%; $P = 0.001$, $df = 102$), while Laurasian taxa (19.5–10 Ma: 2.9%; 10–3.5 Ma: 5.5%; $P = 0.001$, $df = 110$) and northern Andean taxa (10–3.5 Ma: 6%; 19.5–10 Ma: 1.4%; $P = 0.01$, $df = 86$) show the opposite pattern (Fig. 5).

BIOMES

Tropical rainforest (TRFO) and premontane rainforest (PMF) dominate the fossil assemblages, constituting ca. 42% of the assemblage over the entire time studied (Fig. 6, Table 5): TRFO = 20.7% (SD = 11.5), PMF = 19.1% (SD = 11). Lower montane to montane moist/wet forest (MF)

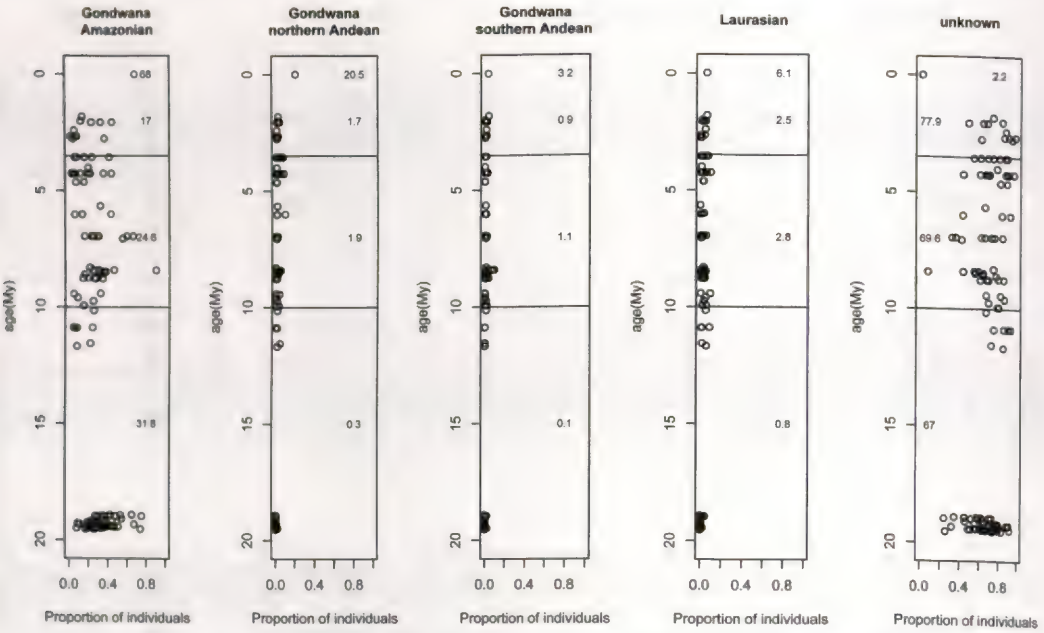

FIGURE 4. Proportion of abundance of individuals per sample that belongs to a given biogeographic affinity. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unknown" mean abundance, given on the left-hand side).

is also important, representing 14.8% (SD = 10.1). Dry biomes represent a very small fraction of the assemblage, and they do not increase significantly over time: tropical dry forest (TDFO) = 2.0% (SD = 3.8), savanna (SV) = 0.4% (SD = 1.1). Freshwater marshes (FW) are present over the entire sequence (FW = 3.4%, SD = 6.6), as are an abundant and constant presence of both mangrove swamps (MG = 8.5%, SD = 13.1) and shallow water marine communities (MR), recognized by the presence of dinoflagellates/foram lining (MR = 0.3%, SD = 1.3) (Fig. 6). Mangroves increased significantly in the last 10 My (> 10 Ma: 4.3%; < 10 Ma: 12.3%; $P = 0.001$, $df = 104$). A large proportion of the taxa remain either unknown as to natural affinities (265 taxa = 53%) or the taxa do not have a preferred biome (104 taxa = 21%), and they correspond to a mean of 65% of the individuals counted per sample (SD = 16.4).

When biomes are analyzed by region (eastern/central/western Panama), the pattern described above does not change substantially. TRFO and PMF do not change when the three areas in Panama are analyzed independently (Fig. 7), and they dominate the assemblage in all three regions. MF is third in dominance in all three regions, but is significantly more abundant in Bocas del Toro and central Panama in the period of 3.5–10 Ma compared to Darien (Bocas del Toro & central Panama 13.9% vs. Darien 8.8%, $P = 0.001$, $df = 10$) (Fig. 7). TDFO and SV are also of very low proportion in all three areas and do not change significantly over time (Fig. 7).

DIVERSITY

There is a significant increase in diversity (rarefied to 80 grains), from an average of 14.5 species per sample in the 10–19.5 Ma interval to 21.2 in the 10–3.5 Ma interval ($P = 0.01$, $df = 110$) (Fig. 8,

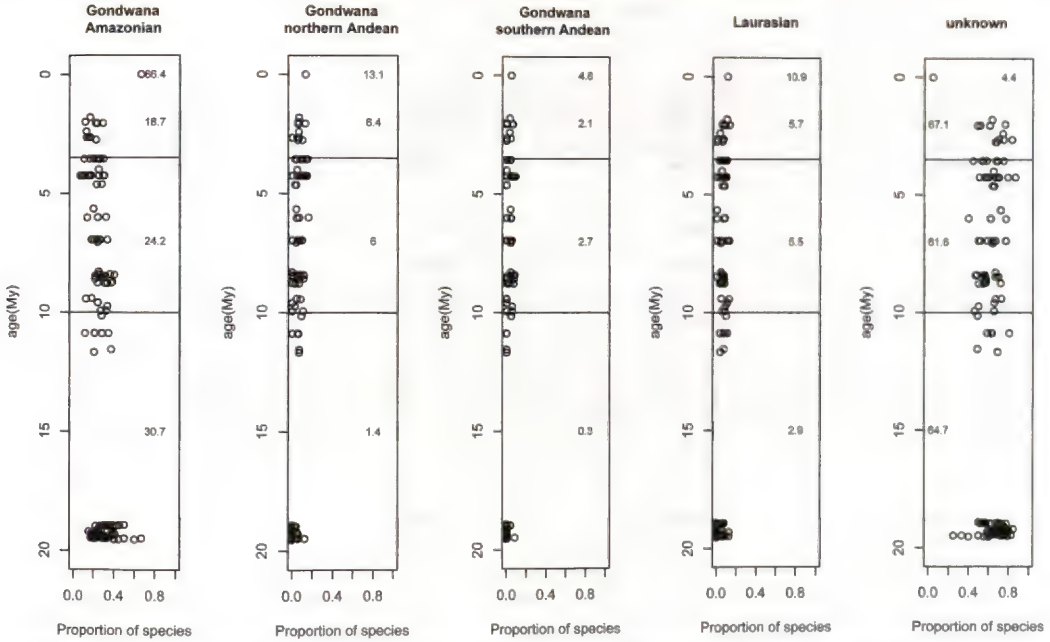

FIGURE 5. Proportion of abundance of species per sample that belongs to a given biogeographic affinity. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unknown" mean abundance, given on the left-hand side).

Table 5). The diversity does not change from 10–3.5 Ma to the < 3.5 Ma interval (< 3.5 = 20.6, $P = 0.7$, $df = 13.1$). The species accumulation curve for each of the three time intervals (Fig. 9) shows a similar pattern, with an initial high slope of species accumulation followed by a lower slope. The 10–19.5 and 3.5–10 Ma intervals have a longer time series than the < 3.5 Ma interval, and both show an increase in the slope again, after a long hiatus of species recovery (6 My in the 10–19.5 Ma interval, and ca. 1 My in the 3.5–10 Ma interval; Fig. 9).

PLANT MACROFOSSILS

Neogene macrofossils from Panama, including wood, leaves, and fruits, were first described by Berry in 1918 and 1921. These fossils were collected during the initial excavations of the Panama Canal but since then, little attention has been given to their floristic affinities. We reexamined Berry's original specimens housed at the National Museum of Natural History (Washington, DC) and present here a revised list of macrofossil taxa from the floras of the Neogene of Panama (Table 6). From these taxa, only leaves, wood, and fruits of Arecaceae and Fabaceae of the Culebra and Gatun formations are accepted. These families were also recognized from pollen by Graham (1988b, 1991a, 1991c). The remaining fossil leaves described by Berry (1918) are poorly preserved and lack distinctive characters for their familial and generic placement. Despite the questionable affinity of the majority of the fossil leaves described by Berry, the physiognomy of these leaves and those in new collections made by the authors, i.e., entire-margined and notophyll to mesophyll in size, suggests warm and probably wet conditions during the Miocene and Pliocene of Panama.

New exposures of the early Middle Miocene Cucaracha Formation (ca. 17–19.5 Ma) from the

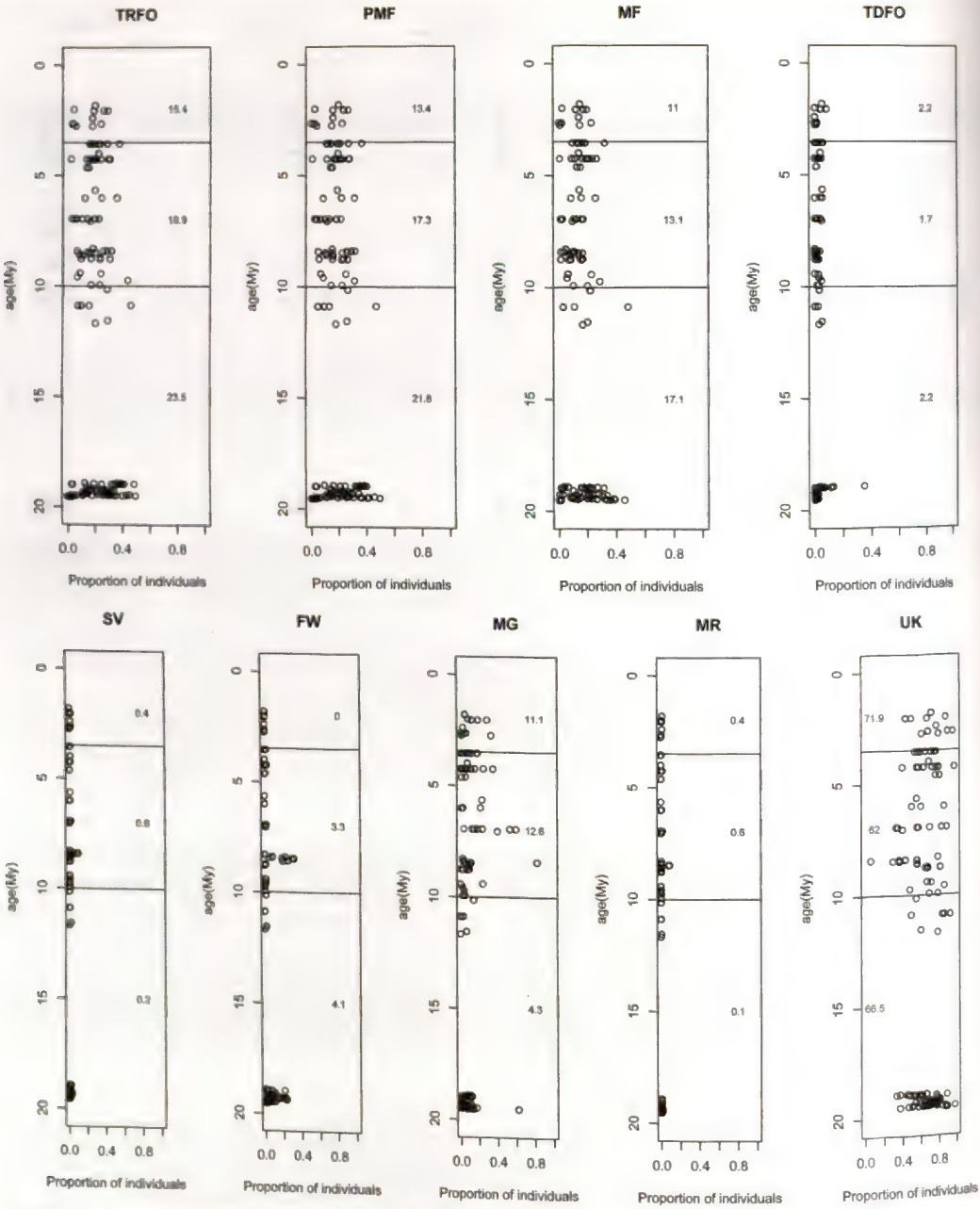

FIGURE 6. Proportion of abundance of individuals per sample that belongs to a particular biome. TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest; SV = savanna; FW = freshwater marsh community; MG = mangrove swamps; MR = shallow water marine community; UK = unassigned. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean abundance per sample is given on the right-hand side (except for "unassigned" mean abundance, given on the left-hand side).

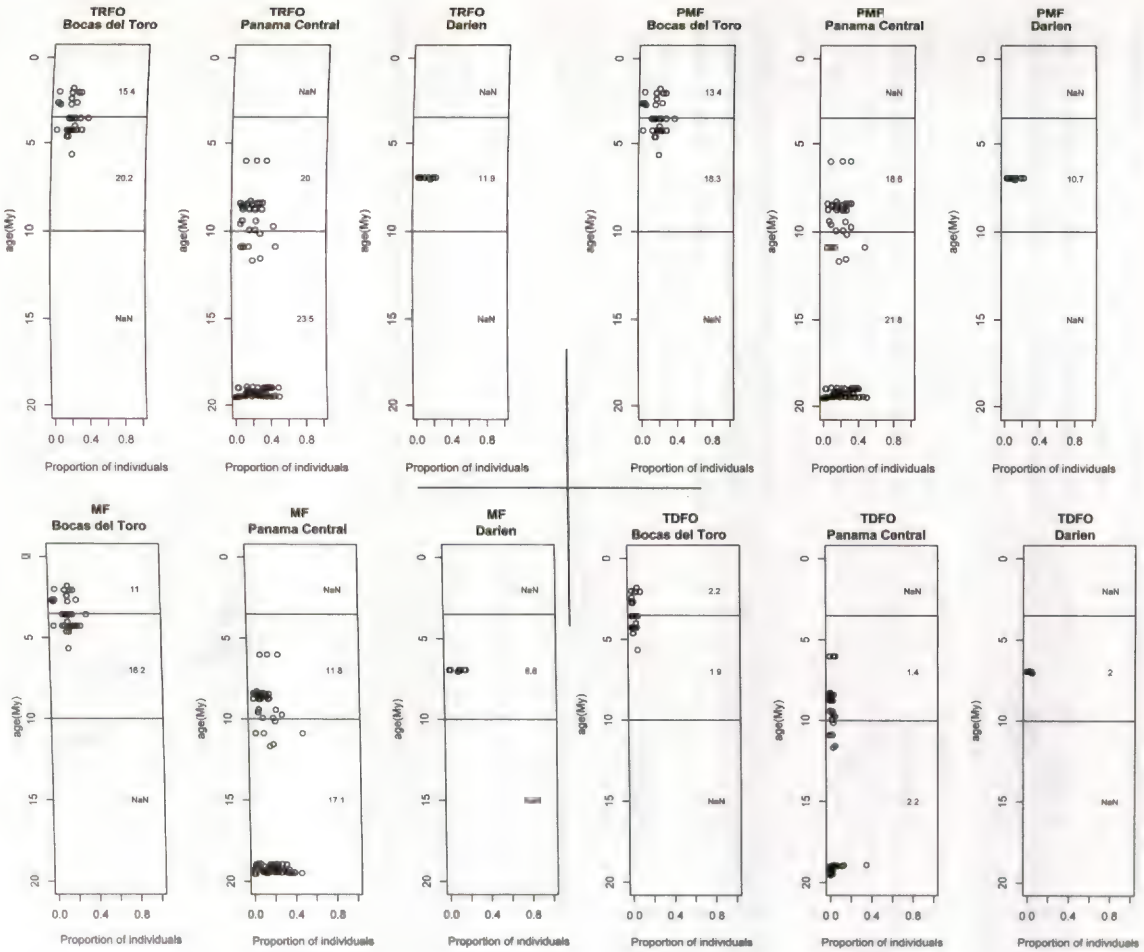

FIGURE 7. Proportion of abundance of individuals per sample that belongs to a given biome, organized by region (Bocas del Toro = western Panama; Darien = eastern Panama). TRFO = tropical wet/moist forest; PMF = premontane wet/moist/rainforest; MF = lower montane to montane moist/wet forest; TDFO = tropical to premontane dry forest.

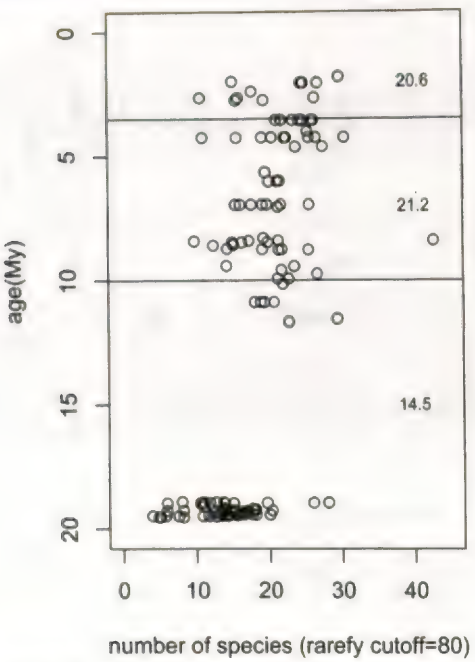

FIGURE 8. Rarefied diversity at a counting level of 80 grains per sample. The sequence is divided into three segments (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma), and for each segment the mean diversity per sample is given on the right-hand side.

Panama Canal have yielded a rich deposit of well-preserved permineralized fruits and seeds (Herrera et al., 2012a; work in progress). These fossils provide additional characters of systematic significance that can facilitate accurate identification to the familial and generic levels in Panamanian macrofloras. Families and genera recognized from this carpoflora include Anacardiaceae (*Spondias* L., *Pentoperculum* Manchester), Annonaceae, Arecaceae, Cannabaceae, Chrysobalanaceae (cf. *Parinari* Aubl.), Euphorbiaceae, Fabaceae, Humiriaceae (*Sacoglottis* Mart.; Herrera et al., 2010), Icacinaceae (Phytocreneae tribe), Juglandaceae (*Oreomunnea* Oerst.), Lauraceae, Menispermaceae, Myristicaceae, Passifloraceae, and Vitaceae (*Cissus* L.). Some of these genera, e.g., *Spondias*, *Parinari*, *Sacoglottis*, and *Cissus*, are recognized for the first time in the Miocene of Panama. New collections of fruits and seeds from the Late Miocene layers of the Gatun Formation include the earliest record of *Vantanea cipaconensis* (Berry) Herrera (Humiriaceae) in Central America, and unidentified specimens of Anacardiaceae and Arecaceae.

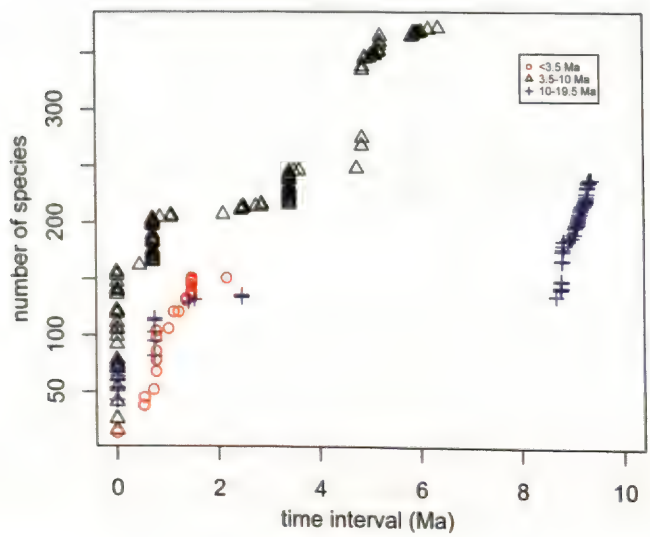

FIGURE 9. Species accumulation curve using the collector's method. There is a curve for each segment (19.5–10 Ma, 10–3.5 Ma, and < 3.5 Ma). The regions of the curves with high slopes are probably due to a sampling artifact, as they are preceded by a sampling hiatus.

TABLE 6. Revised list of plant taxa of Panamanian Neogene floras described by Berry (1918, 1921*).

Taxon	Familial assignment by Berry (1918, 1921)	Current view of the familial/ generic assignment	Formation	Fossil type and comments
Palmoxylon palmacites (Sprengel) Stenzel	Arecaceae	OK	Cucaracha	stem
Iriartites vaughani Berry*	Arecaceae	family provisionally accepted	Gatun	fruit has abundant fibers as seen in modern palms; however, the specimen requires further study
Ficus culebrensis Berry	Moraceae	rejected	Culebra	fossil leaf lacks any distinctive characters
Guatteria culebrensis Berry	Annonaceae	rejected	Culebra, Caimito, and Gatun	leaves; poorly preserved specimens
Myristicophyllum panamense Berry	Myristicaceae	rejected	Culebra	leaf; poorly preserved venation and fragmented
Taenioxylon multiradiatum Felix	Fabaceae	provisionally accepted	Bohio, Culebra, and Cucaracha	wood
Inga oligocenica Berry	Fabaceae	family provisionally accepted	Culebra	the leaf shows crowded basal venation and an asymmetrical base typical of Fabaceae leaves; however, its generic assignment is highly questionable
Cassia culebrensis Berry	Fabaceae	family and genus highly questionable	Culebra	leaf; no common Fabaceae characters present
Hiraea oligocaenica Berry	Malpighiaceae	rejected	Caimito	leaf; poorly preserved venation
Banisteria praenuntia Berry	Malpighiaceae	rejected	Culebra	leaf; poorly preserved venation
Hieronymia lehmannii Engelhardt	Euphorbiaceae	rejected	Caimito	leaf; poorly preserved venation and fragmented
Schmidelia bejucensis Berry	Sapindaceae	rejected	Caimito and Culebra	leaves are entire, pinnate, and eucamptodromous; we do not see any diagnostic characters for placement in Sapindaceae or *Schmidelia* (now Boraginaceae)
Mespilodaphne culebrensis Berry	Lauraceae	rejected	Culebra	leaf; poorly preserved venation and fragmented
Calyptranthes gatunensis Berry	Myrtaceae	family and genus highly questionable	Gatun	similar venation is seen in other families such as Moraceae and Clusiaceae
Melastomites miconioides Berry	Melastomataceae	highly questionable	Culebra	leaf; tertiary veins are not well preserved; it is difficult to differentiate it from leaves in Lauraceae with similar acrodromous venation
Rondeletia goldmanii Berry	Rubiaceae	rejected	Gatun	leaf lacks any distinctive characters
Rubiacites ixoreoides Berry	Rubiaceae	rejected	Gatun	fruit; the specimen shows evidence of germination valves unlike any Rubiaceae fruits

CARBON ISOTOPES

Percentages of total nitrogen (%TN) and total organic carbon (%TOC) display different trends for the marine Culebra Formation and the terrestrial Cucaracha Formation (Fig. 10, Table 7). The %TN varies between 0.09 and 0.13 for the Culebra Formation, whereas %TN ranges between 0.02 and 0.04 for the terrestrial Cucaracha Formation. Similarly, the marine Culebra Formation displays higher TOC percentages than the Cu-

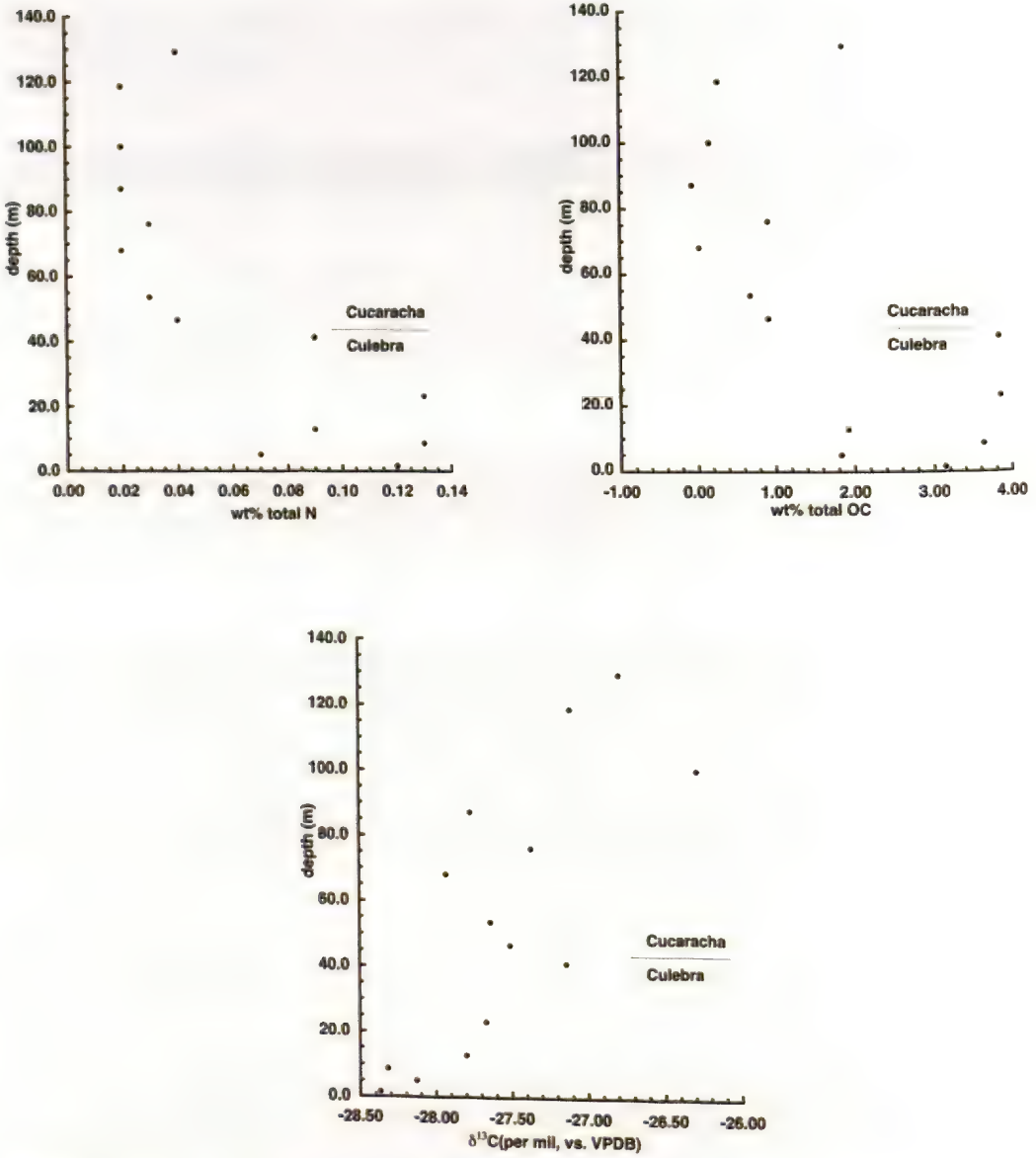

FIGURE 10. Total nitrogen, total organic carbon, and stable carbon isotope values for selected samples from the Cucaracha and Culebra formations. VPDB = Vienna Pee Dee Belemnite.

TABLE 7. Total nitrogen, total carbon (inorganic and organic fractions), and carbon isotope values for 14 selected samples from the Culebra and Cucaracha formations.

	Depth (m)	Sample ID	wt% total N	wt% total C	C/N	wt% total inorganic C	wt% total organic C	$\delta^{13}C$ (permil, vs. VPDB)
Culebra	1.5	CC010046	0.12	3.29	26.17	0.15	3.14	–28.37
	5.0	CC010048	0.07	2.24	26.14	0.41	1.83	–28.13
	8.5	CC010062	0.13	3.76	27.92	0.13	3.63	–28.32
	12.8	CC010052	0.09	2.39	21.33	0.47	1.92	–27.80
	23.0	CC010061	0.13	4.20	29.62	0.35	3.85	–27.67
	41.0	CC010078	0.09	3.86	42.56	0.03	3.83	–27.14
Cucaracha	46.5	CC010095	0.04	1.01	22.75	0.10	0.91	–27.51
	53.5	CC010001	0.03	0.75	22.67	0.07	0.68	–27.64
	68.0	CC010104	0.02	0.20	1.00	0.18	0.02	–27.93
	76.0	CC010008	0.03	0.96	30.33	0.05	0.91	–27.37
	87.0	CC010112	0.02	0.33	0.00	0.40	0.00	—
	100.0	CC010011	0.02	0.20	8.00	0.04	0.16	–26.29
	118.5	CC010012	0.02	0.33	13.50	0.06	0.27	–27.11
	129.0	CC010016	0.04	1.90	46.50	0.04	1.86	–26.79

Abbreviation: VPDB = Vienna Pee Dee Belemnite.

caracha Formation. The %TOC ranges between 1.83 and 3.85 for the Culebra Formation and between 0.00 and 1.86 for the Culebra Formation. Carbon isotope values do not display significant differences between both formations, and values range between –26.29 and –28.37.

DISCUSSION

The Isthmus of Panama represents an excellent opportunity to understand how the vegetation of a newly formed landscape in a tropical setting evolves, because most of the landscape of Panama emerged above sea level only during the last 22 Ma. It was first solely connected to a large land mass (North America) over a long period of time, from 22 to 10 Ma. It was then connected intermittently to a second large mass (South America) from 10 to 3.5 Ma, when the isthmus became permanently connected to both South America and North America. The two connections, however, are not equally balanced. While the North American connection was to a landscape dominated by temperate biomes, the South American connection was to a landscape dominated by tropical biomes.

The new landscape of Panama was formed in a tropical latitude (Montes et al., 2012a, 2012b). But were the earlier floras of Panama dominated by North American (Laurasian) families, when the connection with South America was not fully established until 3.5 Ma ago? The results presented here indicate they were not. Throughout the entire interval studied here (19.5–1.2 Ma) and in the modern flora of Barro Colorado Island, the floras are strongly dominated by Gondwana-Amazonian families, followed by Gondwana-northern Andean, when either the biogeographic affinities of individuals (Fig. 4) or species (Fig. 5) are considered. The Early Miocene macrobotanical record from Panama (Table 2) also indicates an earlier arrival for many South American lineages (e.g., Humiriaceae, Annonaceae, Euphorbiaceae). These results imply that plants were able to cross

the Central American Seaway (CAS, the deep ocean gap that occurred along the tectonic boundary between the South American plate and the Panama microplate) much earlier, at least 10 Ma before other groups, mainly mammals. These results derived from the fossil record were also suggested by Graham in his multiple studies (Graham, 1988a, 1988b, 1991c, 1992, 1999, 2010, 2011), and are also supported by a recent meta-analysis of genetic data of a number of plant clades with members on both sides of the isthmus (Cody et al., 2010) that indicate migrations across CAS much earlier than the traditionally accepted 3.5 Ma final closure of the isthmus. As Cody et al. (2010) pointed out, this could reflect a higher ability of plant disseminules to travel larger distances over water and establish founder populations successfully. These long-distance dispersal events are also interpreted from Late Eocene fruits from the Azuero Peninsula in Panama (Herrera et al., 2012b).

Other recent fossil findings by our intense paleontological exploration in the Canal area have found earlier migrations (ca. 19 Ma) of turtles (Cadena et al., 2012), of snakes (Head et al., 2012), and of crocodiles (Hastings et al., 2013) from South America into Panama across CAS. Genetic evidence also indicates earlier exchanges of bees (Roubik & Camargo, 2012), tree frogs (Pinto-Sanchez et al., 2012), salamanders (Elmer et al., 2013), freshwater *Poecilia* Bloch & Schneider fishes (Alda et al., 2013), and *Amazilia* Lesson hummingbirds (Ornelas et al., 2013). Mammals, on the other hand, do not have an active exchange until much later times, starting at 10 Ma, with an acceleration at 2.7 Ma (Webb, 1976, 2006; Woodburne, 2010). The large variety of mammals found in Panama in the 22–17 Ma interval, including horses, camels, peccaries, bear-dogs, anthracotheriums, rhinocerids, geomyoid rodents, dogs, oreodonts, and protoceratids (Whitmore & Stewart, 1965; Slaughter, 1981; MacFadden & Higgins, 2004; MacFadden, 2006a, 2006b, 2009, 2010; MacFadden et al., 2012; Rincon et al., 2012, 2013), are derived from Laurasian lineages but inhabited the newly formed landscape of Panama that was dominated by a tropical rainforest of Gondwanan origin. Occasionally the same species of mammal (e.g., the rhinoceros *Floridaceras whitei* Wood) was found both in Panama and in Texas and Florida during the Early Miocene, but in contrasting biomes: a temperate forest in North America composed of Laurasian taxa, and a tropical forest in Panama composed mostly of Gondwanan taxa. How did these species interact with the tropical or temperate forest? Were there drastic changes in diet? Or were only generalist mammals able to move into the newly developed tropical forest of Panama? These questions are still open and will require more detailed analyses to be answered.

The dominance of the Gondwanan taxa in the earlier stages of Panama, when the CAS was still active, also underscores the importance of niche conservatism (Wiens & Donoghue, 2004). It was easier for tropical plants to cross the CAS and occupy the lowland tropical Panamanian landscape than for Laurasian temperate taxa to migrate south and shift to a new low-elevation tropical biome. However, some taxa, especially those adapted to montane forests, have Laurasian affinities. Niche conservatism is very strong and has been observed worldwide in a number of biomes (e.g., Crisp et al., 2009) and in the plant fossil record of South America (Jaramillo & Cardenas, 2013).

The extensive work of Graham (1988a, 1988b, 1989, 1991c) indicated that the landscape of Panama was dominated by tropical rainforest, with an associated lower montane and montane forest related to the evolution of the different volcanic arcs that are present in the isthmus (Farris et al., 2011). Graham did not find extensive presence of dry forests or savannas in any part of the sedimentary record. This view is in contrast with the view of Retallack and Kirby (2007), who, from a study of the paleosols of the Cucaracha Formation, inferred an extensive dry habitat for

the Early Miocene of Panama. Our results support Graham's view that the habitats of Panama were strongly dominated by tropical rainforest and montane/lower montane forest, with minimal expansion of dry forest or savanna (Fig. 6).

The carbon isotope record of the Culebra and Cucaracha floras (Fig. 10) also supports the absence of extensive dry conditions. The ratio of total (organic) carbon to total nitrogen (TC/TN) in sediments is used as an indicator of the relative contributions of organic matter from terrestrial versus aquatic sources. Terrestrial organic matter typically possesses TC/TN values > 20, whereas algal organic matter generally displays TC/TN values from 4 to 10 (Meyers, 1994). Physiological differences between C3 and C4 plants result in different carbon isotope signatures (Tipple & Pagani, 2007). C3 plants have a wide range of isotopic values (–20 to –35‰), whereas C4 plants have a narrower range (–10 to –14‰) (Tipple & Pagani, 2007). Thus, the isotopic composition of total organic carbon reflects the relative contribution of terrestrial C3 and C4 plants to the organic matter pool (Huang et al., 1999, 2001; Filley et al., 2001). Results from the continental Cucaracha Formation indicate a dominance of C3 plants, more common to a Neotropical forest than to a tropical grassland ecosystem. Total carbon and total nitrogen values provide further evidence of the continental (i.e., Cucaracha Formation) and mostly marine (i.e., Culebra Formation) depositional environment for these two formations. The absence of extensive C4 savannas also is supported by the carbon isotopic record of mammal enamel that indicate a dominance of C3 plants during the accumulation of the Cucaracha Formation (MacFadden & Higgins, 2004).

The geochemical model used by Retallack and Kirby (2007) to infer dry conditions, the Chemical Index of Alteration without Potash (CIA-K), uses the greater mobility of base cations relative to aluminum oxides during pedogenesis to estimate paleoprecipitation in paleosols. However, this relationship has only been established for temperate climates with a mean annual precipitation (MAP) < 1500 mm and never has been tested in tropical settings. Preliminary attempts to assess this for tropical soils under a MAP > 1500 mm have indicated that there is not a significant correlation of CIA-K with precipitation when tropical soils are included, and the CIA-K should not be applied to tropical settings (Morón et al., 2011).

How did diversity of Panamanian forests fluctuate from the Early Miocene to the present day? Has plant diversity been constantly increasing? Our results indicate that plant diversity was lower in the 10–19 Ma part of the record, and then increased over the past 10 Ma (Fig. 8). However, it is not clear if this pattern is a result of taphonomic artifact. For example, we observed that the sedimentary conditions affect the proportion of pollen grains indicative of mangrove habitats. Lithofacies of the Cucaracha Formation are mostly terrestrial, while lithofacies of the younger formations (Gatún, Chagres, and Bocas del Toro and Darién regions) are shallow marine (Coates et al., 1992, 2003, 2004, 2005; Coates & Obando, 1996; Collins & Coates, 1999; Montes et al., 2012a, 2012b; Hendy, 2013; Pimiento et al., 2013a, 2013b). The taphonomic filtering for plant diversity reconstructions is suggested by the presence of mangroves that increased significantly during the last 10 My in direct association with the sedimentary deposition (Figs. 6, 7) (> 10 Ma: 4.3%; < 10 Ma: 12.3%; $P = 0.001$, $df = 104$). This taphonomic filtering alone may increase the plant diversity in marine samples because the pollen is probably derived from a larger landscape. Therefore, the observed plant diversity in the younger formations studied here would be greater, as it has been noted for modern tropical delta and shallow marine sediments (Muller, 1959; Scheihing & Pfefferkorn, 1984). To fully understand the plant diversity changes seen from the 10–19 Ma to the < 10 Ma records, we would need terrestrial environments in the entire stratigraphic sequence to rule out a possible taphonomic bias.

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APPENDIX 1. Species abundances for extant species of the Barro Colorado Island (BCI) 50-ha plot, 2005 census. —Table A. Summary of the number of individuals and species per family. Each family is assigned to a biogeographic province following Gentry's 1982 classification. —Table B. Species documented from each family and the number of individuals of each.

A. Family summary

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Acanthaceae	2	1	Gondwana-northern Andean
Achariaceae	50	1	Laurasian
Adianthaceae	—	—	unassigned
Amaranthaceae	—	—	unassigned
Anacardiaceae	154	4	Gondwana-Amazonian
Annonaceae	609	7	Gondwana-Amazonian
Anthocerotaceae	—	—	unassigned
Apocynaceae	475	4	Gondwana-Amazonian
Aquifoliaceae	—	—	Laurasian
Araceae	—	—	Gondwana-northern Andean
Araliaceae	68	1	Gondwana-northern Andean
Arecaceae	1279	5	Gondwana-Amazonian
Asteraceae	—	—	Gondwana-northern Andean
Betulaceae	—	—	Laurasian
Bignoniaceae	316	3	Gondwana-southern Andean
Blechnaceae	—	—	unassigned
Bombacoideae	801	7	Gondwana-Amazonian
Boraginaceae	628	3	Laurasian
Bromeliaceae	—	—	Gondwana-northern Andean
Burseraceae	996	6	Gondwana-Amazonian
Byttneroideae	—	—	Gondwana-Amazonian
Cabombaceae	—	—	unassigned
Caesalpinioideae	473	4	Gondwana-Amazonian
Celastraceae	19	1	Laurasian
Chloranthaceae	—	—	Laurasian
Chrysobalanaceae	786	4	Gondwana-Amazonian
Clusiaceae	214	7	Gondwana-northern Andean
Combretaceae	69	2	Gondwana-Amazonian
Connaraceae	—	—	Gondwana-Amazonian
Cucurbitaceae	—	—	unassigned
Cyatheaceae	—	—	unassigned
Cyperaceae	—	—	unassigned
Dilleniaceae	—	—	Gondwana-Amazonian
Dioscoreaceae	—	—	unassigned
Dryopteridaceae	—	—	unassigned
Ebenaceae	17	1	Gondwana-Amazonian
Elaeocarpaceae	67	1	Gondwana-Amazonian
Ericaceae	—	—	Gondwana-northern Andean
Erythroxylaceae	15	1	Dry area Gondwanan group

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Euphorbiaceae	745	12	Gondwana-Amazonian
Fabaceae	—	—	Gondwana-Amazonian
Faboideae	691	13	Gondwana-Amazonian
Fagaceae	—	—	Laurasian
Gentianaceae	—	—	Laurasian
Grewioideae	—	—	Gondwana-Amazonian
Humiriaceae	—	—	Gondwana-Amazonian
Juglandaceae	—	—	Laurasian
Labiatae	—	—	Laurasian
Lacistemataceae	31	1	Gondwana-Amazonian
Lamiaceae	—	—	unassigned
Lauraceae	603	10	Gondwana-Amazonian
Lecythidaceae	619	1	Gondwana-Amazonian
Lentibulariaceae	—	—	unassigned
Loranthaceae	—	—	Gondwana-northern Andean
Lycopodiaceae	—	—	unassigned
Lygodiaceae	—	—	unassigned
Lythraceae	4	1	Laurasian
Malpighiaceae	7	1	Gondwana-Amazonian
Malvaceae	10	1	unassigned
Malvoideae	—	—	unassigned
Marattiaceae	—	—	unassigned
Melastomataceae	85	5	Laurasian
Meliaceae	1939	6	Gondwana-Amazonian
Mimosoideae	453	18	Gondwana-Amazonian
Monimiaceae	26	2	Gondwana-northern Andean
Moraceae	1139	16	Gondwana-Amazonian
Myristicaceae	733	3	Gondwana-Amazonian
Myrtaceae	347	7	Gondwana-southern Andean
Nyctaginaceae	103	1	Gondwana-northern Andean
Nymphaeaceae	—	—	unassigned
Ochnaceae	1	1	Gondwana-Amazonian
Olacaceae	299	2	Gondwana-Amazonian
Onagraceae	—	—	Gondwana-southern Andean
Ophioglossaceae	—	—	unassigned
Phyllanthaceae	—	—	Gondwana-Amazonian
Picramniaceae	37	1	unassigned
Piperaceae	8	1	Gondwana-northern Andean
Poaceae	—	—	unassigned
Podocarpaceae	—	—	Gondwana-southern Andean
Polygalaceae	—	—	Gondwana-Amazonian
Polygonaceae	171	3	unassigned
Polypodiaceae	—	—	unassigned
Pteridaceae	—	—	unassigned
Rhamnaceae	1	1	Laurasian

Family	Number of individuals (BCI 50-ha plot)	Number of species	Biogeographic province or major distributional group
Rhizophoraceae	97	1	Gondwana-Amazonian
Rubiaceae	3395	13	Gondwana-northern Andean
Rutaceae	215	4	unassigned
Salicaceae	373	10	Laurasian
Sapindaceae	99	6	Gondwana-Amazonian
Sapotaceae	348	5	Gondwana-Amazonian
Schizaeaceae	—	—	unassigned
Selaginellaceae	—	—	unassigned
Simaroubaceae	249	2	Gondwana-Amazonian
Solanaceae	12	1	Gondwana-southern Andean
Staphyleaceae	42	1	Laurasian
Sterculiaceae	79	3	Gondwana-Amazonian
Symplocaceae	—	—	Laurasian
Tetrameristaceae	—	—	Gondwana-Amazonian
Tiliaceae	307	4	Gondwana-Amazonian
Ulmaceae	61	2	Laurasian
Urticaceae	454	4	Gondwana-northern Andean
Verbenaceae	18	1	unassigned
Violaceae	1	1	Gondwana-Amazonian
Vochysiaceae	12	1	Gondwana-Amazonian

B. Species summary

Family	Species	Number of individuals (BCI 50-ha plot)
Acanthaceae	*Trichanthera gigantea* (Bonpl.) Nees	2
Achariaceae	*Lindackeria laurina* C. Presl	50
Euphorbiaceae	*Acalypha diversifolia* Jacq.	1
Euphorbiaceae	*Acalypha macrostachya* Jacq.	2
Anacardiaceae	*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels	21
Euphorbiaceae	*Astronium graveolens* Jacq.	37
Anacardiaceae	*Adelia triloba* (Müll. Arg.) Hemsl.	71
Euphorbiaceae	*Spondias mombin* L.	32
Euphorbiaceae	*Alchornea costaricensis* Pax & K. Hoffm.	146
Anacardiaceae	*Alchornea latifolia* Sw.	1
Annonaceae	*Spondias radlkoferi* Donn. Sm.	64
Euphorbiaceae	*Annona acuminata* Saff.	1
Euphorbiaceae	*Croton billbergianus* Müll. Arg.	50
Annonaceae	*Drypetes standleyi* G. L. Webster	318
Euphorbiaceae	*Annona spraguei* Saff.	17
Annonaceae	*Hieronyma alchorneoides* Allemão	40
Annonaceae	*Desmopsis panamensis* (B. L. Rob.) Saff	11
Euphorbiaceae	*Guatteria dumetorum* R. E. Fr.	195
Annonaceae	*Hura crepitans* L.	95
Euphorbiaceae	*Mosannona garwoodii* Chatrou & Welzenis	17
	Margaritaria nobilis L. f.	2

Family	Species	Number of individuals (BCI 50-ha plot)
Euphorbiaceae	*Sapium 'broadleaf'* Jacq.	2
Arecaceae	*Attalea butyracea* (Mutis ex L. f.) Wess. Boer	34
Annonaceae	*Unonopsis pittieri* Saff.	175
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	17
Annonaceae	*Xylopia macrantha* Triana & Planch.	193
Apocynaceae	*Aspidosperma spruceanum* Benth. ex Müll. Arg.	57
Apocynaceae	*Lacmellea panamensis* (Woodson) Markgr.	55
Fabaceae:Caesalpinioideae	*Prioria copaifera* Griseb.	357
Fabaceae:Caesalpinioideae	*Schizolobium parahyba* (Vell.) S. F. Blake	6
Fabaceae:Caesalpinioideae	*Senna dariensis* (Britton & Rose) H. S. Irwin & Barneby	1
Fabaceae:Caesalpinioideae	*Tachigali versicolor* Standl. & L. O. Williams	109
Fabaceae:Mimosoideae	*Abarema macradenia* (Pittier) Barneby & J. W. Grimes	1
Fabaceae:Mimosoideae	*Acacia melanoceras* Beurl.	2
Fabaceae:Mimosoideae	*Cojoba rufescens* (Benth.) Britton & Rose	1
Apocynaceae	*Tabernaemontana arborea* Rose	362
Apocynaceae	*Thevetia ahouai* (L.) A. DC.	1
Fabaceae:Mimosoideae	*Enterolobium schomburgkii* (Benth.) Benth.	4
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	68
Arecaceae	*Astrocaryum standleyanum* L. H. Bailey	160
Fabaceae:Mimosoideae	*Inga acuminata* Benth.	55
Arecaceae	*Oenocarpus mapora* H. Karst.	767
Fabaceae:Mimosoideae	*Inga cocleensis* Pittier	2
Fabaceae:Mimosoideae	*Inga goldmanii* Pittier	32
Fabaceae:Mimosoideae	*Inga laurina* (Sw.) Willd.	8
Fabaceae:Mimosoideae	*Inga marginata* Willd.	102
Fabaceae:Mimosoideae	*Inga nobilis* Willd.	71
Fabaceae:Mimosoideae	*Inga oerstediana* Benth. ex Seem.	2
Arecaceae	*Socratea exorrhiza* (Mart.) H. Wendl.	297
Fabaceae:Mimosoideae	*Inga pezizifera* Benth.	21
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	221
Bignoniaceae	*Tabebuia guayacan* (Seem.) Hemsl.	31
Fabaceae:Mimosoideae	*Inga punctata* Willd.	7
Fabaceae:Mimosoideae	*Inga ruiziana* G. Don	4
Fabaceae:Mimosoideae	*Inga sapindoides* Willd.	72
Fabaceae:Mimosoideae	*Inga spectabilis* (Vahl) Willd.	12
Bignoniaceae	*Tabebuia rosea* (Bertol.) DC.	64
Bombacaceae	*Cavanillesia platanifolia* (Bonpl.) Kunth	18
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	41
Fabaceae:Mimosoideae	*Inga thibaudiana* DC.	45
Fabaceae:Mimosoideae	*Inga umbellifera* (Vahl) Steud.	12
Bombacaceae	*Ochroma pyramidale* (Cav. ex Lam.) Urb.	8
Bombacaceae	*Pachira quinata* (Jacq.) W. S. Alverson	1
Arecaceae	*Elaeis oleifera* (Kunth) Cortés	21
Bombacaceae	*Pachira sessilis* Benth.	10
Bombacaceae	*Pseudobombax septenatum* (Jacq.) Dugand	9

Family	Species	Number of individuals (BCI 50-ha plot)
Bombacaceae	*Quararibea asterolepis* Pittier	714
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	57
Boraginaceae	*Cordia bicolor* A. DC.	323
Fabaceae:Papilionoideae	*Andira inermis* (W. Wright) Kunth ex DC.	32
Boraginaceae	*Cordia lasiocalyx* Pittier	248
Burseraceae	*Protium confusum* (Rose) Pittier	1
Fabaceae:Papilionoideae	*Dipteryx oleifera* Benth.	33
Fabaceae:Papilionoideae	*Erythrina costaricensis* Micheli	18
Fabaceae:Papilionoideae	*Lonchocarpus heptaphyllus* (Poir.) DC.	105
Burseraceae	*Protium costaricense* (Rose) Engl.	111
Burseraceae	*Protium panamense* (Rose) I. M. Johnst.	39
Fabaceae:Papilionoideae	*Myrospermum frutescens* Jacq.	4
Fabaceae:Papilionoideae	*Ormosia amazonica* Ducke	1
Fabaceae:Papilionoideae	*Ormosia coccinea* (Aubl.) Jacks.	6
Burseraceae	*Protium tenuifolium* (Engl.) Engl.	406
Fabaceae:Papilionoideae	*Ormosia macrocalyx* Ducke	4
Fabaceae:Papilionoideae	*Platymiscium pinnatum* (Jacq.) Dugand	47
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	399
Burseraceae	*Trattinnickia aspera* (Standl.) Swart	40
Celastraceae	*Maytenus schippii* Lundell	19
Chrysobalanaceae	*Hirtella americana* L.	3
Chrysobalanaceae	*Hirtella triandra* Sw.	765
Chrysobalanaceae	*Licania hypoleuca* Benth.	11
Chrysobalanaceae	*Licania platypus* (Hemsl.) Fritsch	7
Fabaceae:Papilionoideae	*Platypodium elegans* Vogel	36
Fabaceae:Papilionoideae	*Pterocarpus rohrii* Vahl	53
Clusiaceae	*Calophyllum longifolium* Willd.	44
Clusiaceae	*Chrysochlamys eclipes* L. O. Williams	3
Clusiaceae	*Garcinia intermedia* (Pittier) Hammel	127
Clusiaceae	*Garcinia madruno* (Kunth) Hammel	9
Fabaceae:Papilionoideae	*Swartzia simplex* var. *grandiflora* (Raddi) R. S. Cowan	219
Fabaceae:Papilionoideae	*Swartzia simplex* var. *ochnacea* (DC.) R. S. Cowan	133
Clusiaceae	*Marila laxiflora* Rusby	9
Clusiaceae	*Symphonia globulifera* L. f.	20
Clusiaceae	*Vismia baccifera* (L.) Triana & Planch.	2
Combretaceae	*Terminalia amazonia* (J. F. Gmel.) Exell	27
Combretaceae	*Terminalia oblonga* (Ruiz & Pav.) Steud.	42
Ebenaceae	*Diospyros artanthifolia* Mart.	17
Lacistemataceae	*Lacistema aggregatum* (P. J. Bergius) Rusby	31
Lauraceae	*Beilschmiedia pendula* (Sw.) Hemsl.	270
Lauraceae	*Cinnamomum triplinerve* (Ruiz & Pav.) Kosterm.	14
Lauraceae	*Nectandra 'fuzzy'* Rol. ex Rottb.	1
Lauraceae	*Nectandra cissiflora* Mez & Rusby	31
Lauraceae	*Nectandra lineata* (Kunth) Rohwer	10
Lauraceae	*Nectandra purpurea* (Ruiz & Pav.) Mez	5

Family	Species	Number of individuals (BCI 50-ha plot)
Lauraceae	*Ocotea cernua* (Nees) Mez	26
Lauraceae	*Ocotea oblonga* (Meisn.) Mez	42
Lauraceae	*Ocotea puberula* (Rich.) Nees	21
Lauraceae	*Ocotea whitei* (Rich.) Nees	183
Lecythidaceae	*Gustavia superba* (Kunth) O. Berg	619
Lythraceae	*Lafoensia punicifolia* DC.	4
Malpighiaceae	*Spachea membranacea* Cuatrec.	7
Malvaceae	*Hampea appendiculata* (Donn. Sm.) Standl.	10
Melastomataceae	*Miconia affinis* DC.	6
Melastomataceae	*Miconia argentea* (Sw.) DC.	71
Melastomataceae	*Miconia elata* (Sw.) DC.	1
Melastomataceae	*Miconia hondurensis* Donn. Sm.	6
Melastomataceae	*Miconia prasina* (Sw.) DC.	1
Meliaceae	*Cedrela odorata* L.	2
Meliaceae	*Guarea 'fuzzy'* F. Allam. ex L.	49
Meliaceae	*Guarea grandifolia* DC.	10
Meliaceae	*Guarea guidonia* (L.) Sleumer	359
Meliaceae	*Trichilia pallida* Sw.	90
Meliaceae	*Trichilia tuberculata* (Triana & Planch.) C. DC.	1429
Monimiaceae	*Siparuna guianensis* Aubl.	10
Monimiaceae	*Siparuna pauciflora* (Beurl.) A. DC.	16
Moraceae	*Brosimum alicastrum* Sw.	205
Moraceae	*Ficus costaricana* (Liebm.) Miq.	6
Moraceae	*Ficus insipida* Willd.	1
Moraceae	*Ficus maxima* Mill.	4
Moraceae	*Ficus obtusifolia* Kunth	6
Moraceae	*Ficus popenoei* Standl.	2
Moraceae	*Ficus tonduzii* Standl.	14
Moraceae	*Ficus trigonata* L.	4
Moraceae	*Ficus yoponensis* Desv.	5
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	1
Moraceae	*Maquira guianensis* Aubl.	153
Moraceae	*Perebea xanthochyma* H. Karst.	24
Moraceae	*Poulsenia armata* (Miq.) Standl.	630
Moraceae	*Sorocea affinis* Kunth	19
Moraceae	*Trophis caucana* (Pittier) C. C. Berg	45
Moraceae	*Trophis racemosa* (L.) Urb.	20
Myristicaceae	*Virola multiflora* (Standl.) A. C. Sm.	26
Myristicaceae	*Virola sebifera* Aubl.	559
Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	148
Myrtaceae	*Chamguava schippii* (Standl.) L. R. Landrum	6
Myrtaceae	*Eugenia coloradoensis* Standl.	81
Myrtaceae	*Eugenia galalonensis* (C. Wright ex Griseb.) Krug & Urb.	17
Myrtaceae	*Eugenia nesiotica* Standl.	51
Myrtaceae	*Eugenia oerstediana* O. Berg	187

Family	Species	Number of individuals (BCI 50-ha plot)
Myrtaceae	*Myrcia gatunensis* Standl.	1
Myrtaceae	*Psidium friedrichsthalianum* (O. Berg) Nied.	4
Nyctaginaceae	*Guapira standleyana* Woodson	103
Ochnaceae	*Cespedesia spathulata* (Ruiz & Pav.) Planch.	1
Olacaceae	*Heisteria acuminata* (Bonpl.) Engl.	7
Olacaceae	*Heisteria concinna* Standl.	292
Picramniaceae	*Picramnia latifolia* Tul.	37
Piperaceae	*Piper reticulatum* L.	8
Polygonaceae	*Coccoloba coronata* Jacq.	21
Polygonaceae	*Coccoloba manzinellensis* Beurl.	12
Polygonaceae	*Triplaris cumingiana* Fisch. & C. A. Mey.	138
Rhamnaceae	*Colubrina glandulosa* Perkins	1
Rhizophoraceae	*Cassipourea elliptica* (Sw.) Poir.	97
Rubiaceae	*Alseis blackiana* Hemsl.	1046
Rubiaceae	*Amaioua corymbosa* Kunth	2
Rubiaceae	*Chimarrhis parviflora* Standl.	2
Rubiaceae	*Coussarea curvigemmia* Dwyer	63
Rubiaceae	*Coutarea hexandra* (Jacq.) K. Schum.	1
Rubiaceae	*Faramea occidentalis* (L.) A. Rich.	1909
Rubiaceae	*Genipa americana* L.	21
Rubiaceae	*Guettarda foliacea* Standl.	63
Rubiaceae	*Macrocnemum roseum* (Ruiz & Pav.) Wedd.	24
Rubiaceae	*Posoqueria latifolia* (Rudge) Schult.	12
Rubiaceae	*Psychotria grandis* Sw.	2
Rubiaceae	*Randia armata* (Sw.) DC.	245
Rubiaceae	*Tocoyena pittieri* (Standl.) Standl.	5
Rutaceae	*Zanthoxylum acuminatum* (Sw.) Sw.	29
Rutaceae	*Zanthoxylum ekmanii* (Urb.) Alain	127
Rutaceae	*Zanthoxylum panamense* P. Wilson	58
Rutaceae	*Zanthoxylum setulosum* P. Wilson	1
Salicaceae	*Casearia aculeata* Jacq.	14
Salicaceae	*Casearia arborea* (Rich.) Urb.	75
Salicaceae	*Casearia commersoniana* Cambess.	3
Salicaceae	*Casearia guianensis* (Aubl.) Urb.	1
Salicaceae	*Casearia sylvestris* Sw.	44
Salicaceae	*Hasseltia floribunda* Kunth	182
Salicaceae	*Laetia procera* (Poepp.) Eichler	15
Salicaceae	*Laetia thamnia* L.	26
Salicaceae	*Tetrathylacium johansenii* Standl.	6
Salicaceae	*Zuelania guidonia* (Sw.) Britton & Millsp.	7
Sapindaceae	*Allophylus psilospermus* Radlk.	28
Sapindaceae	*Cupania latifolia* Kunth	12
Sapindaceae	*Cupania rufescens* Triana & Planch.	2
Sapindaceae	*Cupania seemannii* Triana & Planch.	53
Sapindaceae	*Talisia nervosa* Radlk.	1

Family	Species	Number of individuals (BCI 50-ha plot)
Sapindaceae	*Talisia princeps* Oliv.	3
Sapotaceae	*Chrysophyllum argenteum* Jacq.	75
Sapotaceae	*Chrysophyllum cainito* L.	23
Sapotaceae	*Pouteria fossicola* Cronquist	2
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	217
Sapotaceae	*Pouteria stipitata* Cronquist	31
Simaroubaceae	*Quassia amara* L.	5
Simaroubaceae	*Simarouba amara* Aubl.	244
Solanaceae	*Solanum hayesii* Fernald	12
Staphyleaceae	*Turpinia occidentalis* (Sw.) G. Don	42
Sterculiaceae	*Guazuma ulmifolia* Lam.	38
Sterculiaceae	*Sterculia apetala* (Jacq.) H. Karst.	30
Sterculiaceae	*Theobroma cacao* L.	11
Tiliaceae	*Apeiba membranacea* Spruce ex Benth.	205
Tiliaceae	*Apeiba tibourbou* Aubl.	16
Tiliaceae	*Luehea seemannii* Triana & Planch.	85
Tiliaceae	*Trichospermum galeottii* (Turcz.) Kosterm.	1
Ulmaceae	*Celtis schippii* Standl.	42
Ulmaceae	*Trema micrantha* (L.) Blume	19
Urticaceae	*Cecropia insignis* Liebm.	342
Urticaceae	*Cecropia longipes* Pittier	3
Urticaceae	*Cecropia obtusifolia* Bertol.	91
Urticaceae	*Pourouma bicolor* Mart.	18
Verbenaceae	*Aegiphila panamensis* Moldenke	18
Violaceae	*Rinorea sylvatica* (Seem.) Kuntze	1
Vochysiaceae	*Vochysia ferruginea* Mart.	12

APPENDIX 2. Description and illustration of pollen and spore morphotypes.

Morphologic characteristics of the pollen grains were compared with illustrations and descriptions from literature and summarized in Jaramillo and Rueda (2013). Major nomenclatural usages follow those in Jaramillo and Dilcher (2001). Informal species are those between quotation marks; the most important taxa are illustrated in Plates 1 to 11 and brief descriptions are given below. The taxa encountered and their counts are listed in the Supplementary Appendix (available here: <http://dx.doi.org/10.5479/data.stri.jaramillo-2014.>, as well as in Table 4, where possible natural affinities are provided. We have decided to use a nomenclature using fossil names for each taxon, even when the natural affinities are known. This approach is different from that used by Graham in all his publications, where a natural affinity is given as the name of the taxon. We feel that using a fossil taxa naming approach would be more useful when comparing to fossil floras elsewhere in the tropics, where fossil taxa have mostly been used. Also, using natural affinities as the name of a fossil taxon can bring nomenclatural problems in the future because the affinity of a given fossil species can change when further research is done, especially when using SEM and

TEM. It would be more practical to have a morphologically based fossil taxon name with a given natural affinity; that is, a hypothesis of relationship can change over time, but the name of the morphotaxon will not.

We treated 414 morphological fossil species in this appendix; we describe 241 morphologically, which correspond to informal taxa indicated by quotations marks. The other 173 are published and illustrated taxa but not described and correspond to published species. Grain descriptions follow Graham's style and organization: fern spores (trilete and monolete), followed by gymnosperms and angiosperms (monocots and eudicots). Descriptions maintain the Graham format: for pollen grains, form, ambitus, group, apertures, sculpture, exine, and size; for spores, ambitus, group, aperture, sculpture, sporodermis, and size, followed by a tentative modern botanical affinity. The illustrations (Plates 1–11, Figs. 1–399) have a graphic scale that corresponds to 1 cm = 10 µm. Exceptions are indicated directly on the corresponding picture with a special scale bar. Additionally, the slide sample number, microscope coordinate (England Finder), and geological formation are given for each illustration in the figure legend. Most of the microphotographs were taken under oil immersion (×100) using a Pixera (San Jose, California, U.S.A.) System Camera coupled to an Olympus (Tokyo, Japan) BH-2 biological scope. The palynological terminology of the original Graham descriptions has been maintained when possible, and complemented with terms proposed by Punt et al. (2007).

Abbreviations used in the text are as follows: SL = slide sample, EF = England Finder, Amb = ambitus (pollen polar and spore distal face outlines), aff. = similar to, cf. = confer with, Fm. = formation, age = expressed as million years ago (Ma), Ref: = bibliographical reference, ID = identification number that corresponds to the species ID in the public electronic database of Jaramillo and Rueda at <http://biogeodb.stri.si.edu/jaramillo/palynomorph> (Jaramillo & Rueda, 2013). Source of the authorities for extant taxa is Tropicos® (2013).

FERNS: TRILETE SPORES

Anthocerotaceae (Fig. 1). Amb circular; trilete, laesurae inconspicuous, short, thin; finely scabrate, scabrae < 1 µm long, spores displaying ca. 7 depressions fenestrae-like, fenestrae 9–10 µm in diameter; wall ca. 2.5 µm thick; 31–33 µm. Affinity: Pteridophyta, Anthocerotaceae.

Apiculatasporites obscurus. Ref: ID 10011 (Jaramillo & Rueda, 2013); fig. 7 (Graham, 1991a). Affinity: Pteridophyta, Selaginellaceae, *Selaginella* P. Beauv.

Baculatisporites "circularis" (Fig. 2). Amb circular; trilete, laesurae inconspicuous; baculate, baculae slightly dispersed, irregular, sometimes resembling verrucae and short echinae; wall 1 µm thick; ca. 48 µm. Affinity: Pteridophyta.

Baculatisporites "triangularis" (Fig. 3). Amb triangular-obtuse-concave; trilete, laesurae irregular, very thin, inconspicuous, extending to spore margin; baculate, baculae variable, ca. 1.5 µm long at proximal surface to < 1 µm at distal surface; wall < 1 µm thick; 30 µm. Affinity: Pteridophyta.

Baculatriletes "palmiformis" (Fig. 4). Amb circular to triangular-obtuse-convex; trilete, laesurae wide, opened, extending to spore margin; baculate, baculae conspicuous; wall variable, 3 µm thick at proximal surface and 4 µm thick at distal surface; 51 µm. Affinity: Pteridophyta.

Cicatricosisporites "bocatorensis" (Fig. 5). Amb triangular obtuse-convex; trilete; laesurae indistinct; cicatricose; wall 3 µm thick; 46 µm. Ref: figs. 14, 15 (Graham, 1988b). Affinity: Pteridophyta, Pteridaceae, *Ceratopteris* Brongn.

Cingulatisporites psilatus (Fig. 6). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, thin, straight; laevigate; wall thin, < 1 µm thick, conspicuous flange present, smooth, ca. 3.5 µm thick, undulating; 26 µm. Ref: ID 10130 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Cingulatisporites "pteriformis" (Fig. 7). Amb triangular-obtuse-convex; trilete, laesurae extending 3/4 of the distance to spore margin, marginate, margo thick, conspicuous flange present, smooth, 7 µm wide at lateral margins and 5 µm wide at apical margins; laevigate to slightly reticulate; wall 3.5 µm thick at distal surface; 33 µm. Affinity: Pteridophyta, Pteridaceae, *Pteris* L.

Cingulatisporites "rugulatus." Ref: ID 10443 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Cingulatisporites "verrutiformis" (Fig. 8). Amb triangular-obtuse-convex; trilete, laesurae straight, extending to spore margin, spore surrounded by a smooth flange, ca. 5 µm thick; verrucate, verrucae uniform, dense; wall 1 µm thick; 38 µm. Affinity: Pteridophyta.

Concavissimisporites fossulatus (Fig. 9). Amb triangular-obtuse-concave; trilete, laesurae as wide as proximal face; reticulate, brochi variable, resembling foveolate pattern; wall thin, ca. 1 µm thick, surrounded by an irregular smooth flange; 33 µm. Ref: ID 10322 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Concavissimisporites "kyrtomatus" (Fig. 10). Amb triangular-obtuse-concave; trilete, laesurae marginate, extending to spore margin; laevigate at lateral margins and slightly verrucate at apical margins, displaying the kyrtomate condition; wall ca. 2 µm thick; 19 µm. Affinity: Pteridophyta.

Crassoretitriletes vanraadshooveni (Fig. 11). Amb circular; trilete, laesurae extending 2/3 length of spore, straight; foveolate-reticulate, foveolae resembling lumina pattern, variable in shape and size, muri ca. 5 µm wide; wall 5 µm thick, irregular; ca. 74 µm. Ref: ID 10044 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lygodiaceae, *Lygodium microphyllum* (Cav.) R. Br.

Cyatheaceae (*Alsophila*). Ref: figs. 8–11 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae, *Alsophila* R. Br.

Cyatheaceae (*Cnemidaria*). Ref: figs. 12, 13 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae, *Cnemidaria* C. Presl.

Cyatheaceae (Type 1). Ref: fig. 14 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae Type 1.

Cyatheaceae (Type 2). Ref: figs. 15–17 (Graham, 1991a). Affinity: Pteridophyta, Cyatheceae Type 2.

Cyatheacidites annulatus (Fig. 12). Amb circular; trilete; laesurae undulating, extending to spore margin, marginate, margo thin, subtle, laesurae having conspicuous torus; laevigate; wall 1–1.2 µm thick, surrounded by a smooth flange ca. 7 µm thick; 53 µm. Ref: ID 10065 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Dicksoniaceae, *Lophosoria* C. Presl.

Cyathidites "typicus." Ref: figs. 7–9 (Graham, 1988a). Affinity: Pteridophyta, Cyatheceae, *Cyathea* Sm.

Distaverrusporites "usmensis" (Fig. 13). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, ca. 3 µm thick; verrucate, verrucae uniform, dense, generally 3–5 µm in diameter; wall 1 µm thick; 40 µm. Ref: ID 10508 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Echinatisporis muelleri. Ref: ID 10043 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Echitriletes "minispinosus" (Figs. 14, 15). Amb circular to triangular-obtuse-convex; trilete, laesurae irregular, extending to spore margin; echinate, echinae < 1 µm long, uniform; wall < 1 µm thick; ca. 14 µm. Affinity: Pteridophyta.

Echitriletes "minutuechinulatus" (Fig. 16). Amb triangular-obtuse-straight; trilete, laesurae extending to spore margin; echinate, echinae variable, 0.5–1.9 × 0.5–1 µm, conical to cylindrical, pointed-blunted ends, densely distributed; wall 0.8 µm thick; 47 µm. Affinity: Pteridophyta.

Echitriletes "selaginelloides" type *"bacularis"* (Figs. 17, 18). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, thin, marginate, margo thin, inconspicuous; echinate, echinae irregular, having projections resembling baculae and clavae types, 2–5 µm long; wall 1 µm thick; 16.5 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella.*

Echitriletes "selaginelloides" type *"bifurcatus"* (Figs. 19, 20). Amb circular; trilete, laesurae inconspicuous; baculate-echinulate, sculptural elements variable in shape and size, sometimes bifurcated; wall 2.5 µm (excluding ornamentation); ca. 23 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella.*

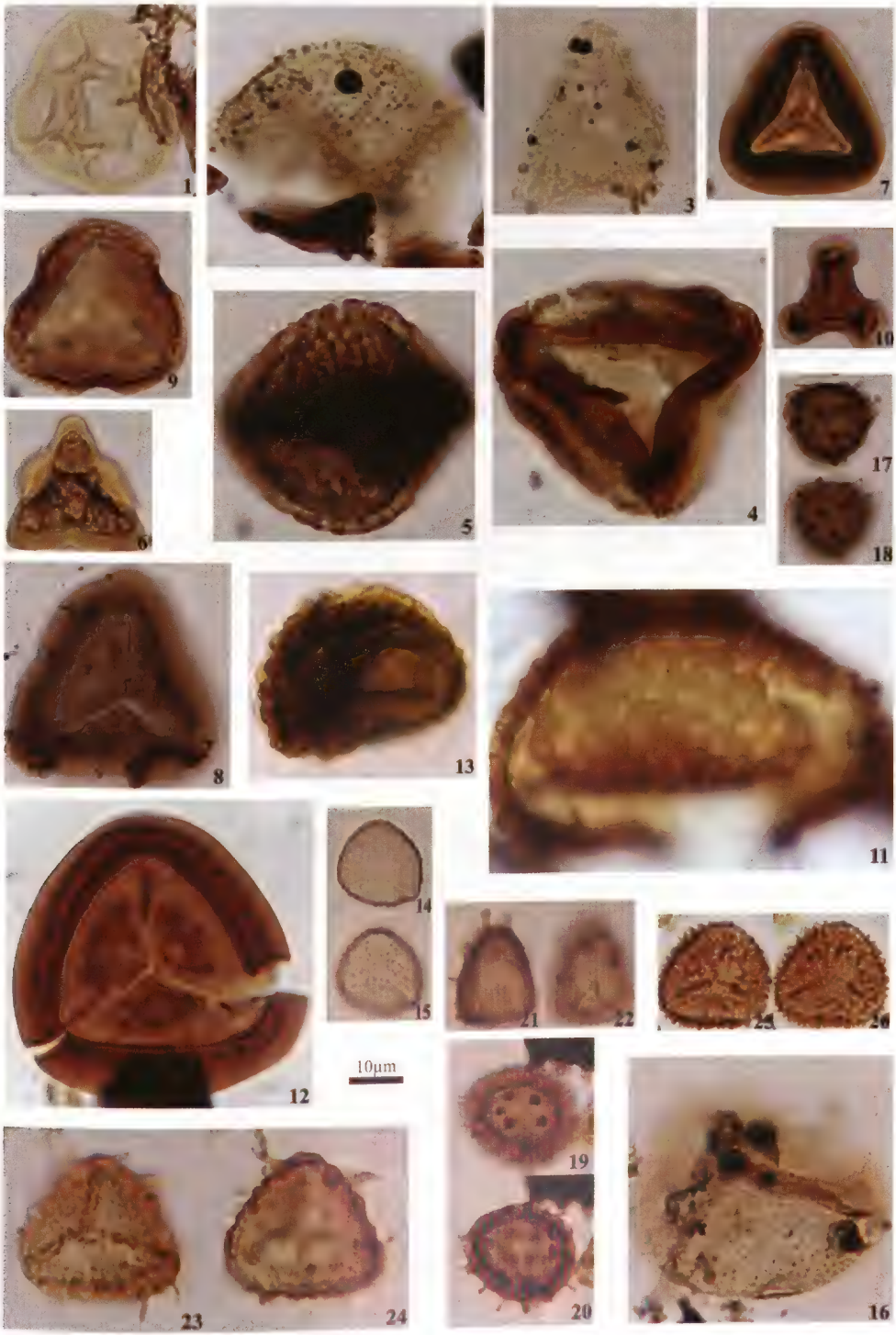
Echitriletes "selaginelloides" type *"echiplanatus"* (Figs. 21, 22). Amb triangular-acute-convex; trilete, laesurae inconspicuous, masked by ornamentation; echinate, echinae variable in size and shape; 18 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella.*

Echitriletes "selaginelloides" type *"muelleri"* (Figs. 23, 24). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo thin, irregular; echinate, echinae variable, 1–5 µm long, dense on proximal surface, apparently verrucate on distal surface; wall 1 µm thick; ca. 29 µm (excluding sculptural elements). Affinity: Pteridophyta, Selaginellaceae, *Selaginella.*

Echitriletes "selaginelloides" type *"regularis"* (Figs. 25, 26). Amb triangular-obtuse-convex; trilete, laesurae thin, inconspicuous, marginate; echinate, echinae 2 × 2 µm, conical, acute ends; wall 1.5 µm thick; 21 µm. Affinity: Selaginellaceae, *Selaginella.*

PLATE 1. Figures 1–26.

1. Anthocerotaceae SL G27/1, EF F18, Shark Hole Point Fm. –4.6 Ma.
2. *Baculatisporites* "circularis" SL 6, EF K-20/2, Chucunaque Fm. –6.95 Ma.
3. *Baculatisporites* "triangularis" SL 174, EF H-35/2, Escudo Veraguas Fm. –2.05 Ma.
4. *Baculatriletes* "palmiformis" SL 174, EF M-36/4, Escudo Veraguas Fm. –2.05 Ma.
5. *Cicatricosisporites* "bocatorensis" SL 196, EF G-28, Shark Hole Point Fm. –4.6 Ma.
6. *Cingulatisporites psilatus* SL 6, EF Y15-2, Gatun Fm. –5.6 Ma.
7. *Cingulatisporites* "pteriformis" SL G26-1, EF D-17, Gatun Fm. –10.02 Ma.
8. *Cingulatisporites* "verrutiformis" SL 18, EF U-41/2, Gatun Fm. –9.4 Ma.
9. *Concavissimisporites fossulatus* SL 68, EF V-17/4, Gatun Fm. –5.6 Ma.
10. *Concavissimisporites* "kyrtomatus" SL 307, EF L3-2, Gatun Fm. –5.6 Ma.
11. *Crassoretitriletes vanraadshooveni* SL 6, EF G-24/3, Chucunaque Fm. –6.95 Ma.
12. *Cyatheacidites annulatus* SL G27-2, EF H-7/2, Gatun Fm. –9.4 Ma.
13. *Distaverrusporites* "usmensis" SL 75.5, EF P-12, Culebra Fm. –19.20 Ma.
14, 15. *Echitriletes* "minispinosus" SL 65, EF H-15/2-4, Cayo Agua Fm. –4.25 Ma.
16. *Echitriletes* "minutuechinulatus" SL 186, EF J-41, Gatun Fm. –9.6 Ma.
17, 18. *Echitriletes* "selaginelloides" type "bacularis" SL G27-2, EF S-47/3, Tuira Fm. –10.15 Ma.
19, 20. *Echitriletes* "selaginelloides" type "bifurcatus" SL G27-1, EF L-5/4, Gatun Fm. –8.9 Ma.
21, 22. *Echitriletes* "selaginelloides" type "echiplanatus" SL 167, EF X-22, Tuira Fm. –12.6 Ma.
23, 24. *Echitriletes* "selaginelloides" type "muelleri" SL 175, EF V-6/2-4, Gatun Fm. –8.9 Ma.
25, 26. *Echitriletes* "selaginelloides" type "regularis" SL 178, EF F-23/4=F24/3, Tuira Fm. –12.6 Ma.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Fossutriletes "*communis*" (Figs. 27, 28). Amb triangular-acute-convex; trilete, laesurae 15 µm long, almost extending to spore margin, marginate, margo 1.8 µm thick; fossulate at distal surface and laevigate at proximal surface; wall 1 µm thick; 27 µm. Affinity: Pteridophyta.

Fossutriletes "*guapissimus*" (Figs. 29, 30). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin; fossulate to foveolate at distal surface, laevigate at proximal surface; wall 2.5 µm thick; 32 µm. Affinity: Pteridophyta.

Foveotriletes "*arrugatus*" (Figs. 31, 32). Amb triangular-acute-straight; trilete, laesurae extending to spore margin; foveolate, foveolae 1 µm wide; wall 3 µm thick; 32 µm. Affinity: Pteridophyta, Ophioglossaceae, *Ophioglossum* L.

Foveotriletes "*laterodepressus*" (Fig. 33). Amb triangular-obtuse-convex; trilete, laesurae straight, almost extending to spore margin, marginate, margo irregular, undulating; foveolate, foveolae 1 µm wide; wall 2 µm thick; ca. 37 µm. Affinity: Pteridophyta.

Foveotriletes ornatus Ref: figs. 26–28 (Graham, 1991a). Affinity: Pteridophyta, trilete fern spores Type 1 & 2.

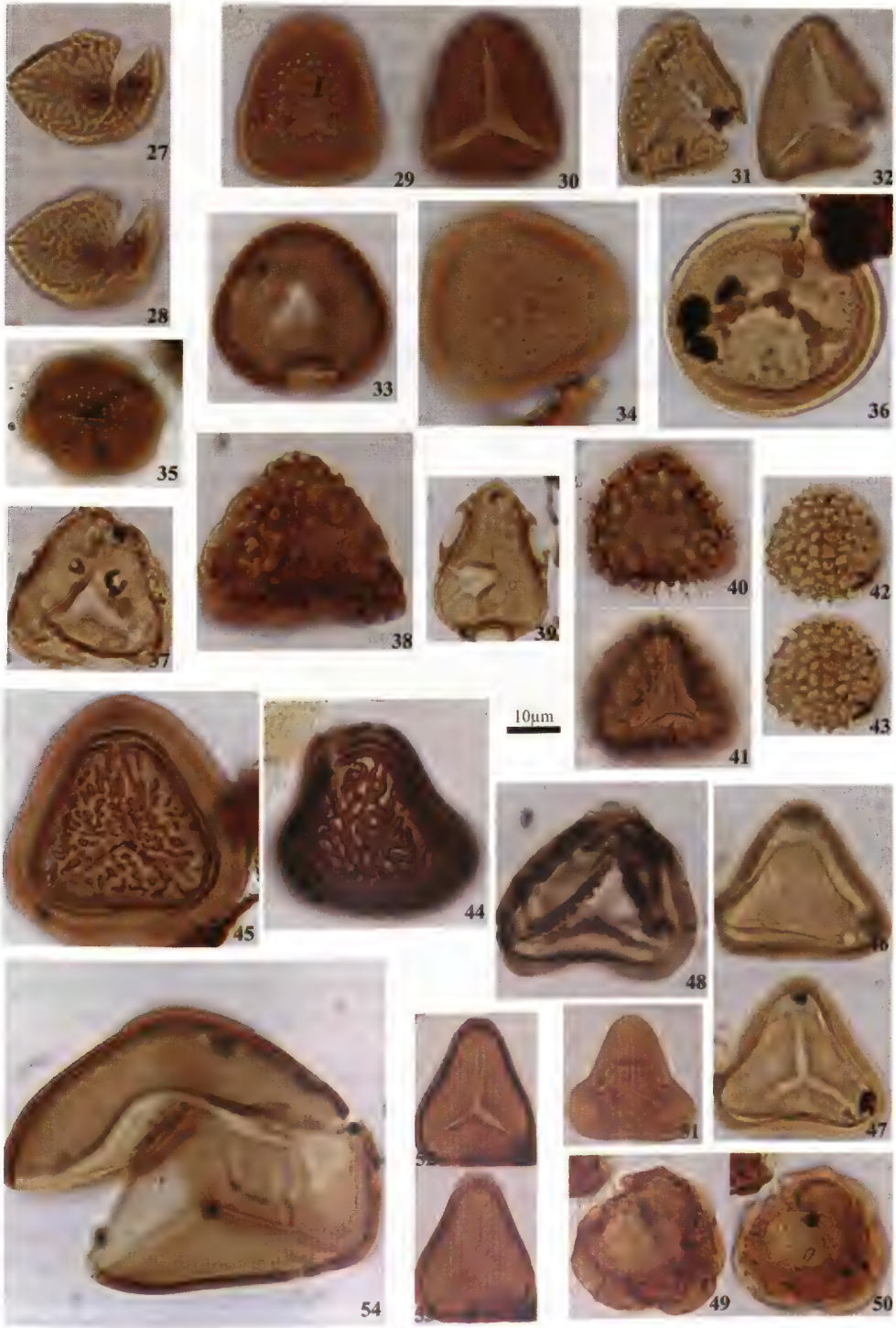
Foveotriletes aff. *ornatus* (Fig. 34). Amb triangular-obtuse-convex; trilete, laesurae straight, acute ends, marginate, margo thin, subtle; foveolate, foveolae resembling punctate pattern, perforations ca. 1 µm in diameter, dispersed; wall < 1 µm thick; 37 µm. Affinity: Pteridophyta.

Foveotriletes "*proximopsilatus*." Ref: figs. 1–3 (Graham, 1988a). Affinity: Pteridophyta, Lycopodiaceae, *Lycopodium* L.

Foveotriletes "*pseudoornatus*" (Fig. 35). Amb triangular-obtuse-concave; trilete, laesurae thin, extending to spore margin, distinct; foveolate, foveolae 1 µm wide; wall 2 µm thick; ca. 28 µm. Ref: ID 10505 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Grammitisporites "*verruminutus*" (Fig. 36). Amb circular; trilete, laesurae extending to spore margin, masked by margo, marginate, margo thick,

PLATE 2. Figures 27–54.
27, 28. *Fossutriletes* "communis" SL G26-1, EF M-11, Gatun Fm. –9.6 Ma.
29, 30. *Fossutriletes* "guapissimus" SL 184, EF E-15/4, Tuira Fm. –10.15 Ma.
31, 32. *Foveotriletes* "arrugatus" SL 370, EF T-62, Tuira Fm. –12.6 Ma.
33. *Foveotriletes* "laterodepressus" SL 2172, EF N-22, Escudo de Veraguas Fm. –2.75 Ma.
34. *Foveotriletes* aff. *ornatus* SL G27-2, EF W-7/2, Tuira Fm. –10.15 Ma.
35. *Foveotriletes* "pseudoornatus" SL Cucaracha 76, EF E-50/2, Cucaracha Fm. –18.85 Ma.
36. *Grammitisporites* "verruminutus" SL 204b, EF L-27/3, Gatun Fm. –8.47 Ma.
37. *Kuylisporites* "irregularis" SL 174, EF J-18/2, Gatun Fm. –9.6 Ma.
38. *Kuylisporites* "multiorodate" SL 187, EF V-24, Cayo Agua Fm. –4.25 Ma.
39. *Kuylisporites waterbolki* SL G26-1, EF N-19/4, Tuira Fm. –10.15 Ma.
40, 41. *Lycopodiumsporites* "clavaelongatus" SL 2172, EF Y-47, Escudo Veraguas Fm. –2.75 Ma.
42, 43. *Lycopodiumsporites* "clavatus" SL 1253, EF C-26/4=D-26/2, Tuira Fm. –6.95Ma.
44. *Nijssenosporites fossulatus* SL G27-1, EF C-16/2, Culebra Fm. –19.40 Ma.
45. *Nijssenosporites* "pteridoides" SL G27-1, EF C-15, Tuira Fm. –10.15 Ma.
46, 47. *Polypodiaceoisporites fossulatus* SL 176, EF Q-10/2, Gatun Fm. –9.6
48. *Polypodiaceoisporites* "reticulatus" SL G26-1, EF T-13/3, Tuira Fm. –12.6 Ma.
49, 50. *Psilatriletes lobatus* SL 174, EF L-15/2, Cayo Agua Fm. –3.55 Ma.
51. *Psilatriletes* sp. < 25 µm SL 27-1, EF C-9, Culebra Fm. –19.46 Ma.
52, 53. *Psilatriletes* sp. 25–50 µm SL G26-1, EF K-17, Culebra Fm. –19.46 Ma.
54. *Psilatriletes* sp. > 50 µm SL 174, EF M-9/2, Escudo Veraguas Fm. –2.5 Ma.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irregular, broken, subtle flange present, smooth; verrucate, verrucae variable; wall ca. 2 µm thick; ca. 41 µm. Ref: fig. 19 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, *Grammitis* Sw.

Kuylisporites "*irregularis*" (Fig. 37). Amb triangular-obtuse-convex; trilete, laesurae extending almost to spore margin, marginate, margo 3.5 µm thick, rounded ends; laevigate; spores displaying irregular perisporium, undulating, cribate, having dispersed and rounded perforations variable in size, ca. 4 µm wide; wall variable, 1.5–2 µm thick; 30 µm. Affinity: Pteridophyta, Cyatheaceae, *Cnemidaria*.

Kuylisporites "*multiorodate*" (Fig. 38). Amb triangular-obtuse-convex; trilete, structure complex, laesurae thin, straight, marginate, margo delimited by sculptural elements; foveolate, resembling areolate condition; wall 3.5 µm thick; 39 µm. Affinity: Pteridophyta, Cyatheaceae.

Kuylisporites waterbolki (Fig. 39). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo thin at ends, increasing at center; laevigate, having irregular and scarce perforations resembling fossulate pattern; spores surrounded by a conspicuous smooth flange, thin at apices, up to 5 µm thick at center, displaying ample apertures as pore-like, ca. 10 µm wide, annulate, sometimes up to three pores laterally; wall 1 µm thick; 35 µm. Ref: ID 10352 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Cyatheaceae, *Hemitelia* R. Br./*Cnemidaria* types.

Lycopodiaceae. Ref: fig. 2 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 1.

Lycopodiaceae. Ref: fig. 3 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 2.

Lycopodiaceae. Ref: figs. 4, 5 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 3.

Lycopodiaceae. Ref: fig. 6 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, Lycopodiaceae, *Lycopodium* Type 4.

Lycopodiumsporites "*clavaelongatus*" (Figs. 40, 41). Amb triangular-obtuse-convex; trilete, laesurae extending almost to spore margin; reticulate, apparently perisporium present, echinate, echinae irregular; wall 1 µm thick; ca. 28 µm. Affinity: Pteridophyta.

Lycopodiumsporites "*clavatus*" (Figs. 42, 43). Amb triangular-obtuse-convex to circular; trilete, laesurae extending to spore margin; reticulate resembling the lopho-reticulate condition, apparently perisporium present, echinate, echinae irregular, thin, acute ends; 23 µm. Affinity: Pteridophyta, Lycopodiaceae, *Lycopodium clavatum* L.

Lycopodiumsporites "*morenoi.*" Ref: ID 10507 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lycopodiaceae.

Lycopodiumsporites sp. Ref: ID 10476 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Lycopodiaceae.

Magnastriatites grandiosus. Ref: ID 10045 (Jaramillo & Rueda, 2013); fig. 20 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Ceratopteris*.

Matonisporites mullerii. Ref: ID 10363 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Nijssenosporites fossulatus (Fig. 44). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, thin, marginate, margo straight, conspicuous flange present, smooth, 4.5 µm thick, displaying external vestigial membrane; rugulate, rugulae thick, wide, sinuous, irregularly rounded at proximal surface, compressed at distal surface; wall 3 µm thick; ca. 38 µm. Ref: ID 10216 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Adianthaceae, *Pityrogramma* Link.

Nijssenosporites "pteridoides" (Fig. 45). Amb triangular-obtuse-convex, rounded apices; trilete, laesurae extending to spore margin, thin, subtle, irregular, undulating, conspicuous flange present, scabrate, 8 µm wide; rugulate, rugulae thick, wide, sinuous, irregularly rounded at proximal surface, compressed at distal surface; wall 3 µm thick; ca. 47 µm. Affinity: Pteridophyta, Pteridaceae, *Pityrogramma*.

Ophioglossaceae (*Ophioglossum*). Ref: fig. 18 (Graham, 1991a). Affinity: Pteridophyta, Ophioglossaceae, *Ophioglossum*.

Planisporites sp. 2. Ref: ID 10013 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiaceoisporites fossulatus (Figs. 46, 47). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, undulating, having conspicuous and irregular verrucae around; verrucate, verrucae flat; wall ca. 1 µm thick, surrounded by smooth flange, ca. 4.5 µm thick; 30–34 µm. Affinity: Pteridophyta.

Polypodiaceoisporites? fossulatus. Ref: ID 10041 (Jaramillo & Rueda, 2013); fig. 21 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris* Type 1.

Polypodiaceoisporites "reticulatus" (Fig. 48). Amb triangular-obtuse-convex; trilete, laesurae wide, triangular, having verrucate processes on margins; laevigate, presence of perisporium on distal surface, reticulate, variable in size; wall ca. 4 µm thick; 39 µm. Affinity: Pteridophyta.

Psilatriletes "brevilaesuratus." Ref: ID 10503 (Jaramillo & Rueda, 2013); figs. 18, 20 (Graham, 1988a), fig. 14 (Graham, 1989). Affinity: Pteridophyta, Pteridaceae, *Antrophyum* Kaulf.

Psilatriletes "enormis." Ref: ID 10504 (Jaramillo & Rueda, 2013); figs. 5, 6, 11, 12, 17 (Graham, 1988a). Affinity: Pteridophyta, Lygodiaceae, *Lygodium* Sw.

Psilatriletes lobatus (Figs. 49, 50). Amb triangular-rounded; trilete, laesurae inconspicuous, thin, short, masked by flange; laevigate; flange variable in size, ca. 1–6 µm thick; wall 1.5 µm thick, surrounded by irregular, undulating, scabrate flange; 30 µm. Ref: ID 10325 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Psilatriletes peruanus. Ref: ID 10326 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Pteridaceae, *Jamesonia* Hook. & Grev., *Pteris rangiferina* Pr. & Miq.

Psilatriletes sp. < 25 µm. (Fig. 51). Amb triangular-obtuse-straight; trilete, laesurae thin, straight, extending 3/4 of the distance to spore margin; laevigate, slightly echinulate at angular areas, resembling a subtle flange; wall 1 µm thick; 22 µm. Ref: ID 10019 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Psilatriletes sp. 25–50 µm. (Figs. 52, 53). Amb triangular-obtuse-straight; trilete, laesurae thin, straight, extending to spore margin, marginate, margo thin at apex and thick at inter-radius areas; laevigate, having subtle granular perispori; wall 2.5 µm thick; 26 µm. Ref: ID 10020 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Cyatheaceae, *Cyathea*.

Psilatriletes sp. > 50 µm. (Fig. 54). Amb triangular-obtuse-convex; trilete, laesurae thin, extending to spore margin, marginate, margo 5 µm wide; laevigate; wall 2.5 µm thick; 65 × 47 µm (distal face). Ref: ID 10021 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Pteridaceae (Type 1). Ref: fig. 21 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 1.

Pteridaceae (Type 2). Ref: fig. 22 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 2.

Pteridaceae (Type 3). Ref: fig. 23 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 3.

Pteridaceae (Type 4). Ref: fig. 24 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 4.

Pteridaceae (Type 5). Ref: fig. 25 (Graham, 1991a). Affinity: Pteridophyta, Pteridaceae, *Pteris*-Type 5.

Retitriletes sommeri. Ref: ID 10052 (Jaramillo & Rueda, 2013); figs. 15, 16 (Graham, 1988a). Affinity: Pteridophyta, Lycopodiaceae, trilete fern spores Type 3.

Rugulatisporites "*irregularis*" (Fig. 55). Amb triangular-obtuse-convex; trilete, laesurae straight, extending 2/3 of the distance to spore margin, acute ends, marginate, margo wider at vertices; laevigate, presence of subtle, irregular and persistent perisporium, rugulate; wall < 1 µm thick; 33 µm. Affinity: Pteridophyta.

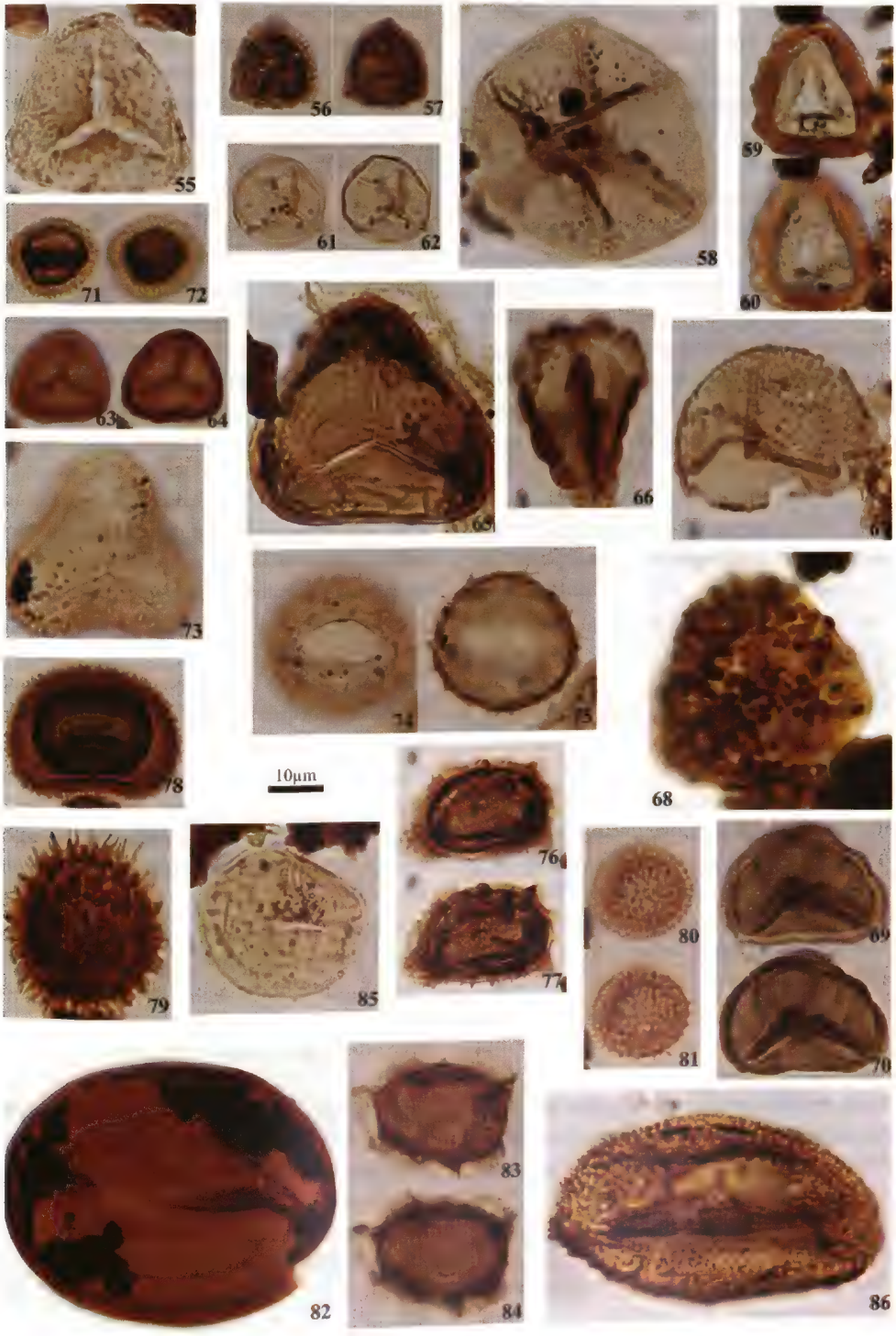
Rugulatisporites "*minutus*" (Figs. 56, 57). Amb triangular-obtuse-convex; trilete, laesurae inconspicuous; rugulate, rugulae irregular, thick, short; wall 2 µm thick; 14 µm. Affinity: Pteridophyta.

Scabratriletes "*complicatus*" (Fig. 58). Amb circular; trilete, laesurae thin, sinuous, acute ends, extending to spore margin, marginate, margo coarse; baculate, baculae small, thin, < 1 µm thick; wall < 1 µm thick; 47 µm. Affinity: Pteridophyta.

Selaginellasporites "*crestatus*" (Figs. 59, 60). Amb triangular-obtuse-convex; trilete, laesurae wide, triangular, extending 2/3 of the distance to spore margin, margins with small granules; laevigate, flange present, displaying margins irregular and serrate to baculate, ca. 4 µm thick; wall < 1 µm thick; 26 × 23 µm (distal face). Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Selaginellasporites "*psilatus*" (Figs. 61, 62). Amb circular; trilete, laesurae irregular, thin, sinuous, extending 3/4 of the distance to spore margin; laevigate; wall 1 µm thick; 16.5 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

PLATE 3. Figures 55–86.
55. *Rugulatisporites* "irregularis" SL G27-2, EF E-19, Gatun Fm. –8.9 Ma.
56, 57. *Rugulatisporites* "minutus" SL 61, EF N-45/1=2, unnamed Fm. –2.65 Ma.
58. *Scabratriletes* "complicatus" SL G26-1, EF P-50, Gatun Fm. –8.9 Ma.
59, 60. *Selaginellasporites* "crestatus" SL 6, EF J-22/2, Gatun Fm. –9.6 Ma.
61, 62. *Selaginellasporites* "psilatus" SL 174, EF R-36/3, Gatun Fm. –9.6 Ma.
63, 64. *Selaginellasporites* "variechinatus" SL 391, EFS-20=T-20, Gatun Fm. –10.05 Ma.
65. *Striatriletes* "saccolomicites" SL 391, EF T-7/2=4, Tuira Fm. –10.15 Ma.
66. *Verrucatotriletes etayoi* SL G26-1, EF L40/4=L41/3, Tuira Fm. –10.15 Ma.
67. *Verrutriletes* "densiverrucatus" SL G27-1, EF E-17, Gatun Fm. –10.05 Ma.
68. *Verrutriletes* "magnoviruelensis" SL Culebra 12.75, EF P-39/2, Culebra Fm. –19.13 Ma.
69, 70. *Verrutriletes* "perforatus" SL 5a, EF F-7/4=G-7/2, Gatun Fm. –5.6 Ma.
71, 72. *Verrutriletes* "uniformis" SL 61, EF Q-20/4, Tuira Fm. –12.6 Ma.
73. *Verrutriletes* "variverrucatus" SL 177, EF K-22/4=K-23/3, Gatun Fm. –8.9 Ma.
74, 75. *Echinomonoletes* "amplimarginatus" SL 6, EF G-17/1, Gatun Fm. –8.4 Ma.
76, 77. *Echinomonoletes* "bifurcatus" SL 20, EF P-21/1, Gatun Fm. –10.0 Ma.
78. *Echinomonoletes* "hirsutus" SL G26-1, EF L-44, Tuira Fm. –10.15 Ma.
79. *Echinomonoletes* "megaechinatus" SL G27-1, EF C-15/4, Tuira Fm. –10.15 Ma.
80, 81. *Echinomonoletes* "sphericus" SL G27-2, EF E-36/1=D-36/3, Tuira Fm. –10.15 Ma.
82. *Laevigatosporites* "magnus" SL 1556, EF T-48/4, Tuira Fm. –6.95 Ma.
83, 84. *Perinomonoletes* "aciculiformis" SL 1253, EF Q-11/4, Tuira Fm. –12.6 Ma.
85. *Perinomonoletes* "microechinulatus" SL 193, EF L-17/2, Tuira Fm. –10.15 Ma.
86. *Perinomonoletes* "minispinosus" SL 349, EF J-15/4, Cayo Agua Fm. –4.25 Ma.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Selaginellasporites "*variechinatus*" (Figs. 63, 64). Amb triangular-obtuse-convex; trilete, laesurae extending to spore margin, marginate, margo ca. 1.5 µm wide, radius 8 µm long; laevigate at proximal surface and echinate at distal surface, echinae 1 µm long, 0.5 µm apart, rounded ends, resembling small baculae; wall 1.5 µm thick; 17 µm. Affinity: Pteridophyta, Selaginellaceae, *Selaginella*.

Striatriletes "*saccolomicites*" (Fig. 65). Amb triangular-obtuse, slightly convex; trilete, laesurae extending 2/3 of the distance to spore margin, straight, thin, marginate, margo wide, straight; rugulate, rugulae variable in size; wall 2.5 µm thick; 44 µm. Affinity: Pteridophyta, Dennstaedtiaceae, *Saccoloma* Kaulf.

Trilete fern spore Type 1. Ref: fig. 26, 27 (Graham, 1991a). Affinity: Pteridophyta.

Trilete fern spore Type 2. Ref: fig. 28 (Graham, 1991a). Affinity: Pteridophyta.

Undulatisporites "*undulapolus*." Ref: ID 10202 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrucatotriletes etayoi (Fig. 66). Amb triangular-obtuse-convex; trilete, laesure thin, straight extending to spore margin, masked by ornamentation; verrucate, verrucae dense, variable, ca. 2–3 × 5–9 µm; wall 2.5 µm thick; 34–36 µm. Ref: ID 10323 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrutriletes "*densiverrucatus*" (Fig. 67). Amb circular; trilete, laesurae thin, extending to spore margin, margins bordered by conspicuous gemmae; gemmate, gemmae irregular, < 1 µm long, grouped in patches resembling "rosettes"; wall 1 µm thick; 38 µm. Affinity: Pteridophyta.

Verrutriletes "*magnoviruelensis*" (Fig. 68). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, ca. 2 µm thick, ends pointed, masked by sculptural elements; verrucate, verrucae variable, 3–4 µm wide, densely distributed over spore surface; wall 2 µm thick; 43 µm. Ref: ID 10330 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Verrutriletes "*perforatus*" (Figs. 69, 70). Amb circular to slightly triangular-obtuse-convex; trilete, laesurae extending to spore margin, straight, marginate; verrucate, verrucae prominent, dense, uniform, resembling the microreticulate pattern; wall 1 µm thick; 28 × 19 µm (distal face). Affinity: Pteridophyta.

Verrutriletes "*uniformis*" (Figs. 71, 72). Amb circular to triangular-obtuse-convex; trilete, laesurae thin, inconspicuous, extending almost to spore margin; probably laevigate, spores having flange, ca. 3.5 µm thick, flange gemmate, gemmae irregular, dense; wall 1 µm thick; 17 µm. Affinity: Pteridophyta.

Verrutriletes "*variverrucatus*" (Fig. 73). Amb triangular-obtuse-concave; trilete, laesurae extending to spore margin, slightly marginate, margo straight; verrucate, verrucae variable, small, elongated, scarce, disperse on spore surfaces; wall ca. 1 µm thick, becoming wider at interangular areas; 25–27 µm. Affinity: Pteridophyta.

Verrutriletes sp. Ref: fig. 19 (Graham, 1988a). Affinity: Trilete fern spore Type 4.

FERNS: MONOLETE SPORES

Dryopteridaceae (*Ctenitis*). Ref: fig. 29 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae, *Ctenitis* (C. Chr.) C. Chr.

Dryopteridaceae Type 1. Ref: fig. 29 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 1.

Dryopteridaceae Type 2. Ref: fig. 30 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 2.

Dryopteridaceae Type 3. Ref: fig. 31 (Graham, 1991a). Affinity: Pteridophyta, Dryopteridaceae Type 3.

Echinosporis "*panamensis*." Ref: ID 10290 (Jaramillo & Rueda, 2013); fig. 21 (Graham, 1988a). Affinity: Pteridophyta, Marattiaceae, *Danaea* Sm.

Echinomonoletes "*amplimarginatus*" (Figs. 74, 75). Biconvex; monolete, laesurae wide, extending 2/3 of the distance to spore margin, marginate, margo thin, inconspicuous; echinate, echinae acute, wide at base, irregular; 28 × 26 µm (proximal face). Affinity: Pteridophyta.

Echinomonoletes "*bifurcatus*" (Figs. 76, 77). Plane-convex; monolete; echinate, echinae 2–5 µm long, irregular ends, crest-like; wall 2 µm thick; 30 × 20 µm (lateral face). Affinity: Pteridophyta.

Echinomonoletes "*hirsutus*" (Fig. 78). Reniform; monolete; echinate, echinae 1.5–2 µm long, < 1 µm wide, densely distributed on surface; wall 1.5 µm thick; 33 µm. Affinity: Pteridophyta.

Echinomonoletes "*megaechinatus*" (Fig. 79). Biconvex; monolete, extending half the distance to spore margin, thin, inconspicuous; echinate, echinae 5 µm long, dense; wall 2 µm thick; 33 µm. Affinity: Pteridophyta, Polypodiaceae.

Echinomonoletes "*sphericus*" (Figs. 80, 81). Plane-convex; monolete; echinate, echinae 2 × 1 µm, acute ends; wall < 1 µm thick; 22 µm. Affinity: Pteridophyta.

Laevigatosporites catanejensis. Ref: ID 10219 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Laevigatosporites "*magnus*" (Fig. 82). Circular; monolete, laesurae extending 3/4 of the distance to spore margin, marginate, margo 3.5 µm thick; laevigate; wall 3 µm thick; 62 × 48 µm (distal face). Affinity: Pteridophyta.

Laevigatosporites tibuensis. Ref: ID 10009 (Jaramillo & Rueda, 2013); figs. 32, 33 (Graham, 1991a). Affinity: Monolete fern spores Types 1 & 2.

Monolete fern spore Type 1. Ref: fig. 32 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 2. Ref: fig. 33 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 3. Ref: fig. 34 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 4. Ref: fig. 35 (Graham, 1991a). Affinity: Pteridophyta.

Monolete fern spore Type 5. Ref: fig. 36 (Graham, 1991a). Affinity: Pteridophyta.

Perinomonoletes "*aciculiformis*" (Figs. 83, 84). Reniform; monolete, laesurae inconspicuous, extending 3/4 of the distance to spore margin; laevigate, spores having perisporium, echinate, undulating, irregular, resembling a reticulate pattern; wall 1 µm thick; 20 × 30 µm (distal face). Affinity: Pteridophyta, Aspleniaceae, *Asplenium* L.

Perinomonoletes "*microechinulatus*" (Fig. 85). Biconvex; monolete, laesurae extending 2/3 of the distance to spore margin, ca. 21 × 3 µm; laevigate, spores having a thin perisporium, echinulate, translucid; wall ca.1 µm thick; 32 × 22 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*minispinosus*" (Fig. 86). Biconvex; monolete, laesurae extending to spore margin, echinate, echinae < 1 µm long, thin; wall ca.

1 µm thick; ca. 52 × 35 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*minutus*" (Fig. 87). Plane-convex; monolete, laesurae inconspicuous; laevigate, spores having perisporium, ca. 1 µm thick, irregular, sessile, resembling the striate pattern; wall 1 µm thick; 26 × 18 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*pseudoreticulatus*" (Fig. 88). Plane-convex; monolete, laesurae simple, extending 2/3 of the distance to spore margin; laevigate, spores having perisporium, irregular, sessile, echinate, echinae 2 µm long, acute ends, resembling a reticulate pattern; wall 1.8–2.4 µm thick; 20 × 14 µm (distal face). Affinity: Pteridophyta.

Perinomonoletes "*reticuloacicularis*." Ref: ID 10350 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiisporites aff. *echinatus* (Fig. 89). Biconvex; monolete, laesurae extending 2/3 of the distance to spore margin, thin; laevigate; subtle flange present, echinate, echinae irregular, variable, wide, rounded ends, sometimes resembling reticulate pattern; wall ca.1 µm thick; 30 µm. Affinity: Pteridophyta.

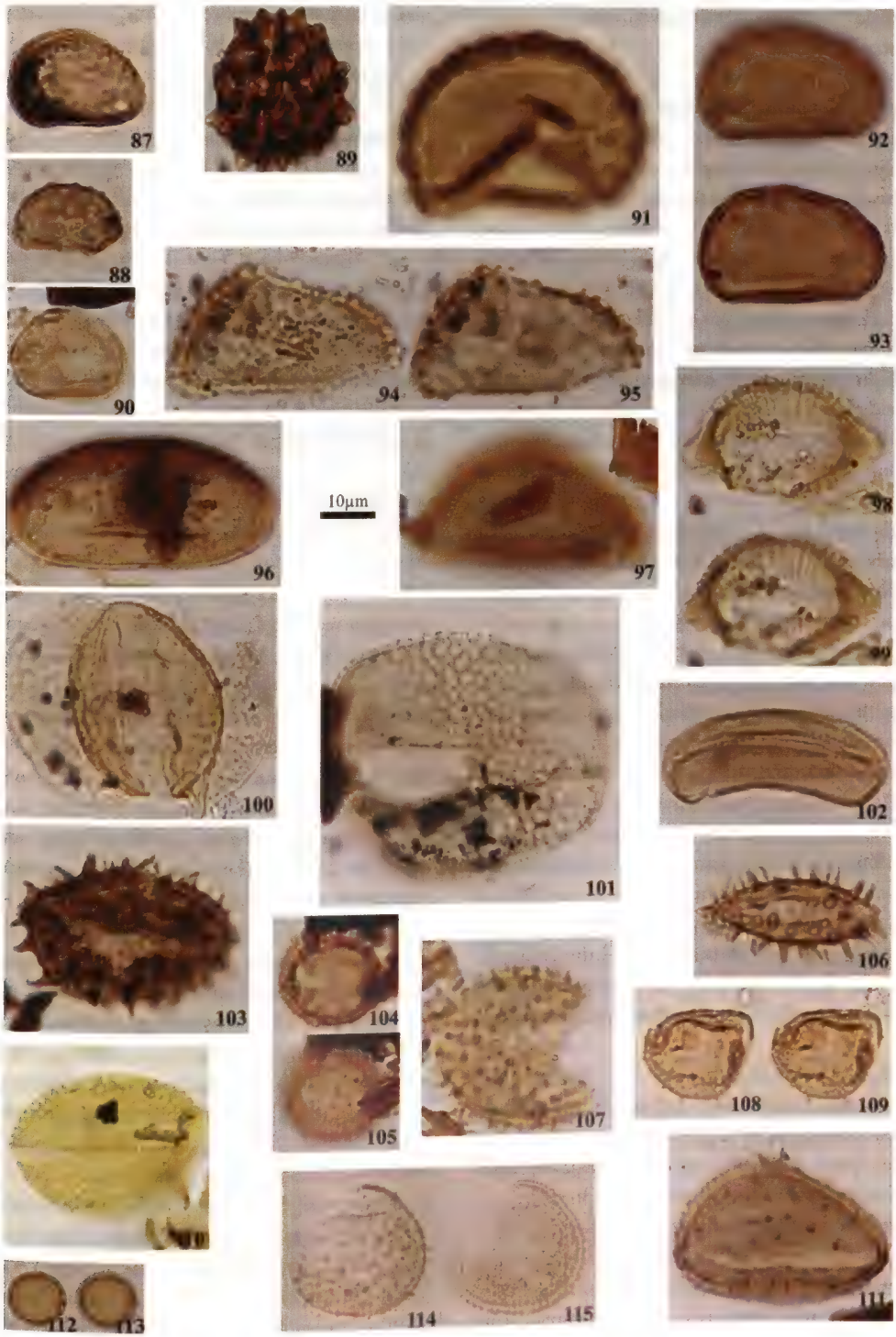
Polypodiisporites "*microverrucate*" (Fig. 90). Reniform; monolete, laesurae extending 3/4 of the distance to spore margin; verrucate at distal surface and laevigate at proximal surface, verrucae small, rounded, resembling small baculae; wall 1–1.2 µm thick; 22.5 × 18 µm. Affinity: Pteridophyta, Polypodiaceae, *Polypodium* L.

Polypodiisporites ? *planus*. Ref: ID 10449 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Polypodiisporites "*reniformis*" (Fig. 91). Reniform; monolete, laesurae extending to spore margin, marginate, margo inconspicuous; verrucate, verrucae rounded to rectangular, variable, 1.5 × 4 µm; wall 3–6 µm thick; 45 × 27 µm (distal face). Affinity: Pteridophyta, Polypodiaceae, *Polypodium*.

Polypodiisporites scabraproximatus. Ref: ID 10031 (Jaramillo & Rueda, 2013) and fig. 33 (Graham,

PLATE 4. Figures 87–115.
87. *Perinomonoletes* "minutus" SL 19, EF G-17/2=4, Gatun Fm. –10.0 Ma.
88. *Perinomonoletes* "pseudoreticulatus" SL 174, EF D-40/3, Tuira Fm. –10.15 Ma.
89. *Polypodiisporites* aff. *echinatus* SL 1241, EF G-68, Tuira Fm. –10.15 Ma.
90. *Polypodiisporites* "microverrucate" SL 174, EF D-22/3, unnamed Fm. –6.95 Ma.
91. *Polypodiisporites* "reniformis" SL 2190, EF U-22/2, Tuira Fm. –10.15 Ma.
92, 93. *Polypodiisporites* "verruplanatus" SL G27-1, EF E-13/1, Tuira Fm. –12.6 Ma.
94, 95. *Polypodiisporites* aff. sp. 2 J & D SL 174, EF F-47/3=G-47/1, Gatun Fm. –5.6 Ma.
96. *Scabramonoletes* "elongatus" SL G26-1, EF S-6/4, Gatun Fm. –8.9 Ma.
97. *Schizaea* "mosquitensis" SL G27-1, EF V-17/1, Escudo Veraguas Fm. –2.05 Ma.
98, 99. *Striatomonoletes* "incertus" SL 175, EF L-5/2=L-6/1, Escudo Veraguas Fm. –2.05 Ma.
100. *Podocarpidites* "globosus" SL Culebra 12.75, EF P-39/2, Culebra Fm. –19.3 Ma.
101. *Bromeliacidites* sp. 1. SL 5b, EF W-19/2=4, Gatun Fm. –8.9 Ma.
102. *Bromeliacidites* sp. 2. SL 65, EF J-9/4, Cayo Agua Fm. –4.25 Ma.
103. *Echimonocolpites* "dariensis" SL 5b, EF Q-21/4, Chucunaque Fm. –6.95 Ma.
104, 105. *Echimonocolpites* "mauritiformis" SL G26-1, EF N-22, Pucro Fm. –6.95 Ma.
106. *Echimonocolpites* "mosquitensis" SL 68, EF L-17, Tuira Fm. –6.95 Ma.
107. *Echimonocolpites* "panamensis" SL 174, EF D-13/1, Tuira Fm. –10.15 Ma.
108, 109. *Echiperiporites* "aquaticus" SL 1620, EF B-25/4=C-26/1, Tuira Fm. –6.95 Ma.
110. *Longapertites* "foveolatus" SL Culebra 3.5, EF Q-44/1, Culebra Fm. –19.40 Ma.
111. *Mauritiidites* "franciscoi" var. "franciscoi" SL 5a, EF J-9/1, Tuira Fm. –12.6 Ma.
112, 113. *Monoporopollenites* "minutus" SL 204, EF R-15/3, Pucro Fm. –6.95 Ma.
114, 115. *Palmapollenites* "iriartoides" SL 175, EF G-23, Tuira Fm. –12.6 Ma.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1991a). Affinity: Pteridophyta, Monolete fern spore Type 2.

Polypodiisporites aff. *speciosus*. Ref: ID 10028 (Jaramillo & Rueda, 2013) and fig. 34 (Graham, 1991a). Affinity: Pteridophyta, Polypodiaceae, *Stenochlaena palustris* (Burm.) Bedd.

Polypodiisporites usmensis. Ref: ID 10046 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta, Blechnaceae, *Stenochlaena palustris*; Dennstaedtiaceae, *Histiopteris incisa* (Thunb.) J. Sm.; Polypodiaceae, *Phlebodium aureum* (L.) J. Sm.

Polypodiisporites "*verruplanatus*" (Figs. 92, 93). Reniform; monolete, laesurae thin, extending to spore margin; verrucate, verrucae irregular in shape and size, 3–7 µm wide, decreasing toward proximal surface; wall 1 µm thick; 34 × 21 µm (distal face). Affinity: Pteridophyta.

Polypodiisporites aff. sp. 2 J & D (Figs. 94, 95). Plano-convex; monolete, laesurae thin, extending to spore margin; verrucate, verrucae irregular, 1–5 µm wide; wall 2.5 µm thick; 24 × 45.5 µm (lateral face). Ref: ID 10034 (Jaramillo & Rueda, 2013). Affinity: Pteridophyta.

Scabramonoletes "*elongatus*" (Fig. 96). Plane-convex; monolete, laesurae thin, straight, extending half distance to spore margin, ca. 24 µm long, marginate, margo subtle, thin; scabrate, displaying irregular and dispersed granules; wall 1 µm thick; 50 × 24 µm (distal face). Affinity: Pteridophyta.

Schizaea "*mosquitensis*" (Fig. 97). Plane-convex; monolete, laesurae masked by folded wall; cingulated, cingulum ca. 3.5 µm thick, reticulate, muri thin, lumina rounded; wall < 1 µm thick; 44 × 23 µm (distal face). Affinity: Pteridophyta, Schizaeaceae, *Schizaea* Sm.

Striatomonoletes "*incertus*" (Figs. 98, 99). Biconvex; monolete, laesurae extending to spore margin; striate, striae oriented from distal to proximal surface, dense, wide; wall 2 µm thick; 30 × 18 µm (distal face). Affinity: Pteridophyta.

GYMNOSPERMS

Podocarpidites "*globosus*" (Fig. 100). Bisaccate, inaperturate; body amb circular, psilate to finely scabrate, 20 µm, body wall 3.5 µm thick; air sacs two, hemispheric, psilate, translucid, angularly oriented; overall dimension (including air sacs) 48 µm. Ref: fig. 37 (Graham, 1991a). Affinity: Gymnospermae, Podocarpaceae, *Podocarpus* L'Hér. ex Pers.

ANGIOSPERMS: MONOCOTS

Arecipites "*perfectus*." Ref: ID 2036 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Arecipites regio. Ref: ID 34 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Bromeliacidites sp. 1 (Fig. 101). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain, margins masked by reticulum; reticulate, lumina variable, 2–4 µm wide, muri 1 µm thick, simplicolumellate; tectate, wall 2 µm thick; 57 × 47 µm. Affinity: Monocotyledoneae, Bromeliaceae.

Bromeliacidites sp. 2 (Fig. 102). Amb elliptic; monocolpate, colpus thin, extending nearly entire length of grain, margins masked by small baculae; baculate, baculae short, dense, ca. 1 µm thick; apparently intectate, wall 1.2 µm thick; 43 × 16 µm. Affinity: Monocotyledoneae, Bromeliaceae, *Catopsis* Griseb.

Cyperaceae. Ref: ID 228 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Cyperaceae.

Dioscorea/*Rajania*. Ref: ID 236 (Jaramillo & Rueda, 2013); fig. 51 (Graham, 1988a). Affinity:

Monocotyledoneae, Dioscoreaceae, *Dioscorea* L./ *Rajania* L. types.

Echimonocolpites "*dariensis*" (Fig. 103). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; echinate-verrucate, echinae acute, irregular, wide at base, surface between echinae filled by small, dense, and variable verrucae; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 43 × 27 µm (excluding ornamentation). Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*mauritiformis*" (Figs. 104, 105). Amb circular, monocolpate, colpus wide, extending 2/3 length of grain; echinate, echinae acute, thin with rounded and wide base, ca. 1 µm thick; tectate, wall 1 µm thick; 21 × 17 µm. Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*mosquitensis*" (Fig. 106). Amb elliptic; monocolpate, colpus extending nearly entire length of grain, wide, bordered by sculptural elements; echinate, echinae irregular and dispersed, 3–6 µm long; intectate, wall 1 µm thick, nexine 1 µm thick (excluding ornamentation); 33 × 15 µm. Affinity: Monocotyledoneae, Arecaceae.

Echimonocolpites "*panamensis*" (Fig. 107). Amb circular, monocolpate, colpus extending nearly entire length of grain, thin, irregular, with margins not well defined; echinate, echinae acute, pyramidal, slightly depressed, 1.5–2.5 µm tall; tectate, wall < 1 µm thick (excluding ornamentation); 24 µm. Affinity: Monocotyledoneae, Arecaceae, cf. *Mauritia* L. f. (similar to *Mauritia*, but *Mauritia* has been reported as porate).

Echiperiporites "*aquaticus*" (Figs. 108, 109). Spherical, amb circular; periporate, pores 8, circular, 2.5 µm wide, annulate; echinate, echinae conical, sharp, wider at base, 1.5 µm long; tectate, wall 2.5 µm thick (including echinae); 25 µm. Affinity: Monocotyledoneae, Alismataceae, *Echinodorus* Rich.

Foveomonocolpites "*panamensis*." Ref: ID 2090 (Jaramillo & Rueda, 2013); figs. 33, 34 (Graham, 1988a). Affinity: Monocotyledoneae, Arecaceae, *Desmoncus* Mart. type.

Longapertites "*foveolatus*" (Fig. 110). Amb elliptic; monocolpate, colpus extending nearly entire length of grain, straight, thin; foveolate, foveolae uniform; tectate; ca. 33 µm. Ref: figs. 29–32 (Graham, 1988a); fig. 19 (Graham, 1988b). Affinity: Monocotyledoneae, Arecaceae, *Cryosophila* Blume.

Mauritiidites "*franciscoi*" var. "*franciscoi*" (Fig. 111). Amb elliptic, monocolpate, colpus wide, extending nearly entire length of grain; echinate, echinae acute, conical-based, appearing as inserted into slightly ectexine concavity, 3 µm long; tectate, wall 1.2 µm thick (excluding ornamentation); 41 × 28 µm. Ref: ID 469 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Mauritia flexuosa* L. f.

Mauritiidites franciscoi var. *minutus*. Ref: ID 470 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Mauritia*.

Monocolpopollenites "*canalensis*." Ref: ID 2092 (Jaramillo & Rueda, 2013); figs. 35, 36 (Graham, 1988a); figs. 28, 29 (Graham, 1989). Affinity: Monocotyledoneae, Arecaceae, *Synechanthus* H. Wendl.

Monoporopollenites annulatus. Ref: ID 487 (Jaramillo & Rueda, 2013); fig. 38 (Graham, 1991a). Affinity: Monocotyledoneae, Poaceae.

Monoporopollenites "*minutus*" (Figs. 112, 113). Spherical, amb circular; monoporate, pore circular, ca. 1 µm wide, displaying subtle annulus; psilate; tectate, wall 1 µm thick, tectum 0.5 µm

thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 12 µm. Affinity: Monocotyledoneae, Poaceae.

Palmae Type 1. Ref: figs. 39, 40 (Graham, 1991a). Affinity: Monocotyledoneae, Arecaceae.

Palmapollenites "*iriartoides*" (Figs. 114, 115). Amb elliptic; monocolpate, colpus inconspicuous, irregular, thin; clavate, clavae variable, 1–1.5 µm long, scarce, irregularly distributed; intectate, wall < 1 µm thick, columellae 0.5 µm tall, nexine 0.5 µm thick; 29 µm. Affinity: Arecaceae, *Iriartea deltoidea* Ruiz & Pav.

Palmapollenites "*microperforatus*." Ref: figs. 41, 42 (Graham, 1991a). Affinity: Monocotyledoneae, Arecaceae, *Oenocarpus* Mart., Palmae Type 2.

Palmapollenites "*phytelephensis*" (Fig. 116). Amb elliptic, monocolpate, colpus extending 2/3 length of grain; apparently reticulate, resembling the micropitted condition, lumina < 1 µm wide; tectate; 51 µm. Affinity: Monocotyledoneae, Arecaceae, *Phytelephas* Ruiz & Pav.

Palmapollenites "*scheeleaensis*" (Fig. 117). Amb elliptic; monocolpate, colpus irregular, thin, extending nearly entire length of grain; apparently verrucate, columellae grouping as small packages resembling verrucate pattern; tectate, wall 2 µm thick, strongly columellate, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 45 × 26 µm. Affinity: Monocotyledoneae, Arecaceae, *Scheelea zonensis* L. H. Bailey.

Psilamonocolpites amazonicus. Ref: ID 978 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae, *Euterpe* Mart.

Psilamonocolpites "*longiformis*" (Fig. 118). Amb elliptic; monocolpate, colpus thin, extending nearly entire length of grain; psilate; tectate, wall 1 µm thick; 60 × 18 µm. Affinity: Monocotyledoneae, Araceae.

Psilamonocolpites medius (Fig. 119). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; psilate; tectate, wall 1 µm thick; 41 µm. Ref: ID 593 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Psilamonocolpites rinconii (Fig. 120). Amb elliptic; monocolpate, colpus wide, extending nearly entire length of grain; reticulate, lumina < 1 µm wide, fine; tectate, wall 1 µm thick, densely columellate; 26 µm. Ref: ID 1031 (Jaramillo & Rueda, 2013). Affinity: Monocotyledoneae, Arecaceae.

Retimonocolpites "*heteroretifossulatus*." Ref: ID 2091 (Jaramillo & Rueda, 2013); figs. 20–22 (Graham, 1988b); figs. 25–27 (Graham, 1989). Affinity: Monocotyledoneae, Arecaceae, *Manicaria* Gaertn. type.

Retimonocolpites "*palmatus*" (Figs. 121, 122). Amb circular, slightly elliptic; monocolpate, colpus wide, straight, extending nearly entire length of grain; reticulate, lumina variable, 1–1.5 µm wide, decreasing toward aperture, rounded, muri thick, simplicolumellate; tectate, wall 1 µm thick; 24 × 18 µm. Affinity: Monocotyledoneae, Arecaceae, *Cryosophila*.

Retipollenites "*minutus*" (Figs. 123, 124). Spherical, amb circular; inaperturate; reticulate, lumina 1 µm wide; tectate, wall 1 µm thick, densely columellate, columellae baculae-shaped; 12 µm. Affinity: Monocotyledoneae, Araceae.

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Acanthaceae aff. "*hygrophilensis*" (Fig. 125). Suboblate, amb circular; stephanocolporate, approximately 10 to 12 colpi, equatorially arranged, equidistant, thin, straight, extending nearly entire length of grain; pores inconspicuous, not seen in polar view; baculate, baculae irregular; intectate, wall 2 µm thick, sexine 1 µm thick, nexine 1 µm thick, columellae 1 µm thick, tectum

absent; 21 µm. Affinity: Dicotyledonae, Acanthaceae, *Hygrophila guianensis* Nees.

Alnipollenites verus (Fig. 126). Suboblate, amb circular; stephanoporate, pores 5, vestibulate, circular, 3–4 µm wide; psilate; tectate, wall 1–2 µm thick, densely columellate; 18–20 µm. Ref: ID 15 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Betulaceae, *Alnus* Mill.

Anacardiaceae "*morenensis*" (Figs. 127, 128). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, straight, extending nearly entire length of grain, apparently having costae colpi 5–6 µm wide; pore oblongate, becoming circular, 4 µm wide; striato-reticulate, striae not well defined, thin, longitudinally oriented, lumina uniform, < 1 µm wide; tectate, wall 2 µm thick, sexine 1 µm thick, nexine 1 µm thick, tectum 1 µm thick; 26 × 18 µm wide. Affinity: Dicotyledonae, Anacardiaceae, *Spondias* L.

Annonaceae (*Cymbopetalum*). Ref: figs. 1, 2 (Graham, 1991b). Affinity: Dicotyledonae, Annonaceae, *Cymbopetalum* Benth.

Baculipollenites "*inciertus*" (Fig. 129). Suboblate, amb circular-triangular-convex, trilobate; tricolporate, equatorially arranged, equidistant, thin, acute, extending 3/4 length of grain, pores apparently endexinic, protruding; baculate, baculae < 1 µm tall; tectate, wall ca. 1.2 µm thick at intercolpium area, 2 µm at colpus area; 39 µm. Affinity: Dicotyledonae.

"Bignoniaceae" Type (Figs. 130, 131). Suboblate, amb circular-triangular-convex; tricolporate, equatorially arranged, equidistant, thin, acute, extending 3/4 length of grain, pores circular, 5 µm wide; scabrate, scabrae < 1 µm tall; tectate, wall ca. 1.5 µm thick; 22 × 24 µm. Affinity: Dicotyledonae, Bignoniaceae, *Tabebuia* Gomes ex DC.

Bombacaceae (cf. *Aguiaria*). Ref: fig. 30 (Graham, 1989); fig. 6 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae-Bombacoideae, *Aguiaria* Ducke.

Bombacacidites araracuarensis. Ref: fig. 34 (Graham, 1989); fig. 9 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Ceiba* Mill.

Bombacacidites baculatus (Fig. 132). Oblate, amb triangular-obtuse-straight; tricolporate, colpi equatorially arranged, equidistant, short, pointed ends, pores inconspicuous, circular; reticulate, lumina variable, scrobiculate at polar areas, diminishing from 2 µm (polar area) to < 0.5 µm wide at equatorial interaperture areas, muri simplicolumellate, free bacuale at apertures; semitectate, wall 1–2.5 µm thick; 50 µm (polar diameter). Ref: ID 55 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Pachira aquatica* Aubl.

Bombacacidites "*bombacopsiformis*" (Figs. 133, 134). Oblate, amb triangular-obtuse-straight; tricolporate, colpi equatorially arranged, equidistant, short, pointed ends, pores inconspicuous, apparently protruding, small; reticulate, lumina diminishing from 2 µm (polar area) to < 0.5 µm wide (equatorial interaperture areas), muri simplicolumellate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 27 µm (polar diameter). Ref: fig. 7 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Bombacopsis* Pittier/*Bernoullia* Oliv. types.

Bombacacidites brevis (Figs. 135, 136). Oblate, amb circular; apparently tricolporate, colpi equatorially arranged, equidistant, short, rounded ends, pores inconspicuous, small, annulate, lolongate; reticulate, lumina < 1 µm wide (equatorial interaperture areas), muri simplicolumellate, columellae dense; tectate, wall < 1 µm thick; 20 µm (polar diameter). Ref: fig. 108 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 10.

Bombacacidites "colpiechinatus" (Fig. 137). Oblate, amb triangular-obtuse-convex; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, indistinct; pores inconspicuous, echinate, echinae short, scarcely distributed; tectate; 21 × 24 µm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae.

Bombacacidites nacimientoensis. Ref: fig. 7 (Graham, 1991b). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Bernoullia.*

Bombacacidites "problematicus" (Figs. 138, 139). Oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short; reticulate, lumina variable, mesocolpium psilate to micropitted; tectate; 20 × 28 µm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae.

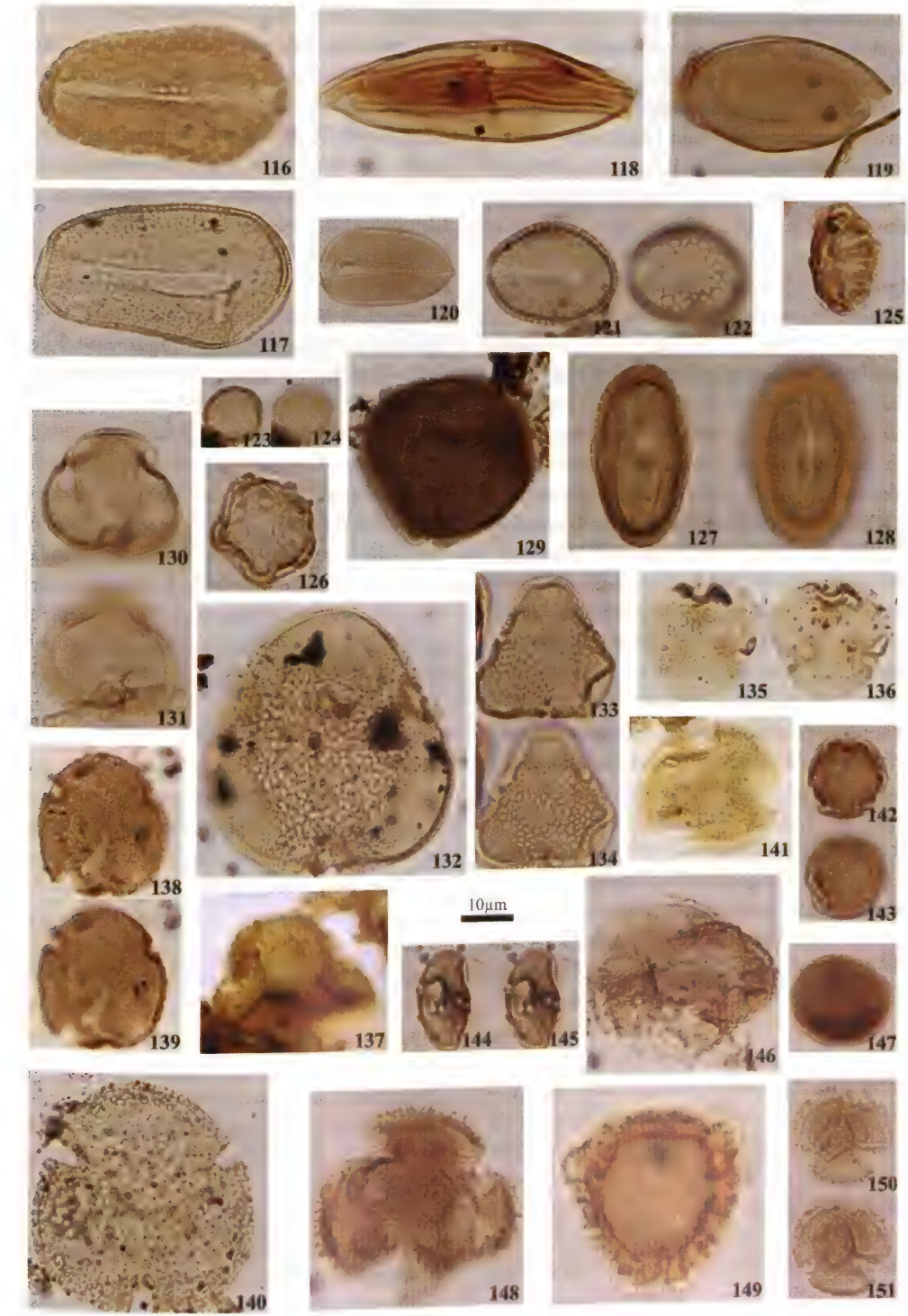
Bombacacidites "pseudobombiformis" (Fig. 140). Oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, acute ends, pores inconspicuous, small; reticulate, lumina homogeneous, fine, 1 µm wide, muri simplicolumellate; tectate, wall 1.5 µm thick; 44 µm (polar diameter). Ref: fig. 8 (Graham, 1991b); fig. 35 (Graham, 1989). Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Pseudobombax septenatum* (Jacq.) Dugand.

Brevitricolpites "panamensis" (Fig. 141). Spherical, amb circular; tricolpate, colpi equatorially arranged, equidistant, short, wide, margins straight, ends pointed, costate, margo 4 × 1 µm; baculate, baculae short, rounded; intectate, wall 1 µm thick; 27.5 µm. Affinity: Dicotyledonae.

Brevitricolpites "triangulatus." Ref: fig. 91 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 9.

Brevitricolpites "scabratus" (Figs. 142, 143). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, straight, short,

PLATE 5. Figures 116–151.
116. *Palmapollenites* "phytelephensis" SL G29-2, EF O-13, Gatun Fm. –9.6 Ma.
117. *Palmapollenites* "scheeleaensis" SL 17, EF H-14/4, Tuira Fm. –6.95 Ma.
118. *Psilamonocolpites* "longiformis" SL 158, EF N-10/2=4, Gatun Fm. –8.6 Ma.
119. *Psilamonocolpites medius* SL 174, EF M-15/1, Gatun Fm. –10.0 Ma.
120. *Psilamonocolpites rinconii* SL 4, EF A-9/4, Gatun Fm. –9.6 Ma.
121, 122. *Retimonocolpites* "palmatus" SL 5a, EF J-21/2, Gatun Fm. –10.2 Ma.
123, 124. *Retipollenites* "minutus" SL 175, EF J-35/1, Gatun Fm. –9.6 Ma.
125. *Acanthaceae* aff. "hygrophilensis" SL 178, EF W-10/2, Escudo Veraguas Fm. –2.05 Ma.
126. *Alnipollenites verus* SL 210, EF X-35/2, Gatun Fm. –9.6 Ma.
127, 128. *Anacardiaceae* "morenensis" SL 2165, EF W-22/1=2, Escudo Veraguas Fm. –2.05 Ma.
129. *Baculipollenites* "inciertus" SL G26-1, EF J-18/1, Gatun Fm. –5.6 Ma.
130, 131. "Bignoniaceae" Type SL 175/6, EF U-21/4, Gatun Fm. –10.0 Ma.
132. *Bombacacidites baculatus* SL 193, EF H-15/4, Chucunaque Fm. –7.05 Ma.
133, 134. *Bombacacidites* "bombacopsiformis" SL 178, EF U-9/1, Gatun Fm. –5.6 Ma.
135, 136. *Bombacacidites brevis* SL 193, EF E-22/4, Chagres Fm. –10.0 Ma.
137. *Bombacacidites* "colpiechinatus" SL Cucaracha 56.5, EF S-47/1, Cucaracha Fm. –18.93 Ma.
138, 139. *Bombacacidites* "problematicus" SL 1620, EF H-36/1, Gatun Fm. –10.2 Ma.
140. *Bombacacidites* "pseudobombiformis" SL 193, EF Y-22/1, Gatun Fm. –5.6 Ma.
141. *Brevitricolpites* "panamensis" SL La Boca 37.5, EF E-47/2, Culebra Fm. –19.20 Ma.
142, 143. *Brevitricolpites* "scabratus" SL 168, EF C-21/4, Gatun Fm. –5.6 Ma.
144, 145. *Burseraceae* "protiumensis" SL 174, EF C-39/3, Gatun Fm. –10.2 Ma.
146. *Chelonanthus* type SL 5a, EF S-25/3, Gatun Fm. –5.6 Ma.
147. *Clavainaperturites microclavatus* SL G26-1, EF L-7/2, Gatun Fm. –10.2 Ma.
148. *Clavapollenites* "circularis" SL G27-2, EF F-19/1, Cayo Agua Fm. –4.25 Ma.
149. *Clavapollenites* "triangulatus" SL 60, EF Q-10/1, Cayo Agua Fm. –4.25 Ma.
150, 151. *Clavatricolpites* "infinitus" SL G26-1, EF N-52/4, Gatun Fm. –10.0 Ma.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inconspicuous, pores elongated, short, becoming lineal, ca. 3 µm long; verrucate-perforate, showing variable and small verrucae with small perforation betwen them resembling rugulate pattern, verrucae variable, 1–1.5 µm tall; tectate, wall 2 µm thick, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 14 µm. Affinity: Dicotyledonae, Fabaceae.

Brevitricolpites sp. Ref: fig. 96–98 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 8.

Burseraceae "*protiumensis*" (Figs. 144, 145). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, extending nearly entire length of grain, straight, pore elongated-oblongate, ca. 4 × 8 µm; reticulate, muri simplicolumellate, columellae thin, dense; tectate, wall variable, 1 µm thick at polar area and 2 µm thick at aperture areas, tectum 1 µm thick, sexine 1 µm thick, nexine 1 µm thick; 19–20 × 12–16.5 µm. Affinity: Dicotyledonae, Burseraceae, *Protium* Burm. f.

Cabombaceae (*Cabomba*). Ref: fig. 38 (Graham, 1991b). Affinity: Dicotyledonae, Cabombaceae, *Cabomba* Aubl.

Chelonanthus type (Fig. 146). Lineal and crossed tetrad; individual grains oblate (compressed in tetrad), amb circular; triporate, pores adjacent at contact areas between grains, circular, 2 µm wide, annulate, annulus thin; reticulate, lumina variable, 1–2.5 µm wide, muri thin, simplibacullate; tectate, wall 1 µm thick; individual grains 26 µm, tetrad 38 µm. Affinity: Dicotyledonae, Gentianaceae, *Chelonanthus alatus* (Aubl.) Pulle.

Cichoreacidites longispinosus Ref: ID 318 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Liguliflorae type.

Clavainaperturites clavatus Ref: ID 152 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Clavainaperturites microclavatus (Fig. 147). Spherical, amb circular; inaperturate; clavate, clavae resembling small and fine baculae < 1 µm tall; intectate, wall 1 µm thick; 20 µm. Ref: ID 1056 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Chloranthaceae, *Hedyosmum* Sw.

Clavapollenites "*circularis*" (Fig. 148). Spherical, amb circular-trilobate; tricolpate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, with margins bordered by baculae; clavate-baculate, baculae ca. 1.5 µm tall; intectate, wall ca. 2.5 µm thick, exhibiting dense and uniform baculae; 38 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Clavapollenites "*triangulatus*" (Fig. 149). Amb triangular-obtuse-convex; tricolporate, colpi equatorially arranged, equidistant, short, pore indistinct; reticulate, lumina variable, 2–4 µm wide, muri curvimurate, simplicolumellate, columellae ca. 2.5 µm long; semitectate, wall 4 µm thick; 38 µm. Affinity: Dicotyledonae.

Clavatricolpites "*infinitus*" (Figs. 150, 151). Subprolate, amb circular; tricolpate, colpi equatorially arranged, equidistant, wide, deep, extending 3/4 length of grain, pores inconspicuous; clavate, having irregular and dispersed clavae not longer than 1 µm; intectate, wall 1.5 thick; 19 µm. Affinity: Dicotyledonae.

Clavatricolpites "*tectatum.*" Ref: ID 915 (Jaramillo & Rueda, 2013); figs. 55–58 (Graham, 1988a). Affinity: Dicotyledonae, Euphorbiaceae, *Tetrorchidium* Poepp.

Combretaceae (cf. *Bucida*). Ref: figs. 10, 11 (Graham, 1991b). Affinity: Dicotyledonae, Combretaceae, cf. *Bucida* L.

Compositae (Mutisieae type). Ref: fig. 14 (Graham, 1991b). Affinity: Dicotyledonae, Asteraceae, Mutisieae type.

Corsinipollenites psilatus (Fig. 152). Suboblate, amb circular; triporate, pores circular, annulate, inconspicuous, protruding, coarse; scabrate; tectate, wall variable, 3 µm thick at intercolporium area to 7 µm thick at aperture; 27 µm. Ref: ID 175 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Onagraceae, *Ludwigia* L.

Crassiectoapertites columbianus (Fig. 153). Suboblate, amb circular-triangular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, straight, wide, acute ends, almost joined at apices, pore inconspicuous, probably circular; psilate; tectate, wall 4 µm thick; 47 µm. Ref: ID 180 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Dioclea reflexa* Hook. f.

Cricotriporites aff. *macroporus*. Ref: ID 198 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Cricotriporites "*minimus*" (Figs. 154, 155). Spherical, amb circular; triporate, pore equatorially arranged, equidistant, circular, annulate; psilate, intectate; 8 µm. Affinity: Dicotyledonae.

Crototricolpites "*euphorbiensis*" (Figs. 156, 157). Subprolate, amb circular; tricolpate, colpi equatorially arranged, equidistant, inconspicuous, masked by sculptural elements; clavate-verrucate, clavae short, resembling verrucae pattern, uniform; intectate, wall ca. 1 µm thick; 34 × 25 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Crototricolpites "*pseudodaemoni*" (Figs. 158, 159). Spheroidal, amb circular; tricolpate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, inconspicuous; clavate, clavae resembling the crotonoid pattern, 1–1.5 µm high, > 1 µm wide, irregular, becoming baculae or gemmae; intectate, wall > 1 µm thick; 23 µm. Affinity: Dicotyledonae, Euphorbiaceae.

Cucurbitaceae Type (Fig. 160). Spherical, amb circular; periporate, pores 4 to 6, inconspicuous, circular, wide, annulate; baculate-echinate, baculae short, thin, echinae rounded, conical, ca. 5 × 2 µm; intectate, wall 6 µm thick; 52 µm. Affinity: Dicotyledonae, Cucurbitaceae.

Echiperiporites akanthos (Figs. 161, 162). Spherical, amb circular; periporate, 6 pores, uniformly distributed, appearing as equatorial area resembling stephanoporate condition, pores circular, 1.5 µm wide, annulate, annulus 1 µm thick; echinate, echinae conical, sharp, wide at base, short, ca. 1 µm long; tectate, wall 1.5 µm thick; ca. 23 µm. Affinity: Dicotyledonae.

Echiperiporites estelae (Fig. 163). Spherical, amb circular; periporate, > 20 pores, uniformly distributed, pores circular, 3.5 µm wide, annulate, annulus 2 µm thick; echinate-scabrate, echinae acute, ca. 5 µm long, wide at base; tectate, wall 3 µm thick; ca. 45 µm. Ref: ID 251 (Jaramillo & Rueda, 2013); fig. 36 (Graham, 1991b); figs. 59, 60 (Graham, 1988a). Affinity: Dicotyledonae, Malvaceae–Malvoideae, *Thespesia populnea* (L.) Sol. ex Corrêa, *Hibiscus tiliaceus* L., *Hampea* Schltdl./*Hibiscus* L. types; Convolvulaceae, *Ipomoea* L.

Echiperiporites "*ipomoensis*" (Figs. 164, 165). Spherical, amb circular; periporate, pores uniformly distributed, equidistant, circular, 3–4 µm wide; echinate, surface between echinae scabrate; tectate, wall 1.5–2 µm thick, columellae baculae-shaped; 35–44 µm. Affinity: Dicotyledonae, Convolvulaceae, *Ipomoea* L.

Echiperiporites "*pantagruelicus*" (Fig. 166). Spherical, amb circular; periporate, pores uniformly distributed, equidistant pores circular; echinate, echinae 15–17 µm long, uniformly arranged on surface; tectate, wall 5 µm thick, columellae 1 µm long, size increasing under the spines, tectum 0.5 µm thick, sexine 1.5 µm thick, nexine 4 µm thick; ca. 100 µm. Affinity: Dicotyledonae, Malvaceae.

Echiperiporites sp. Ref: fig. 81 (Graham, 1988b). Affinity: Dicotyledonae, Unknown 1.

Echitricolporites "chiquitinus" (Figs. 167–169). Prolate-spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, thin, pore indistinct, probably elongated, small; echinate, echinae acute, 2 µm tall; tectate, wall 3 µm thick (including ornamentation); 13 × 11.5 µm. Affinity: Dicotyledonae, Asteraceae.

Echitricolporites mcneillyi. Ref: ID 261 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae.

Echitricolporites "microspinosus" (Figs. 170, 171). Subprolate, amb circular, becoming spheroidal; tricolporate, colpi equatorially arranged, equidistant, short, wide, not well defined, having irregular margo interrupted at equator, pores elongated-oblongate; echinate, echinae short, scarce, acute, wide at base; tectate, wall 2.5 µm thick (including ornamentation); 26 × 24 µm. Affinity: Dicotyledonae, Boraginaceae, *Cordia* L.

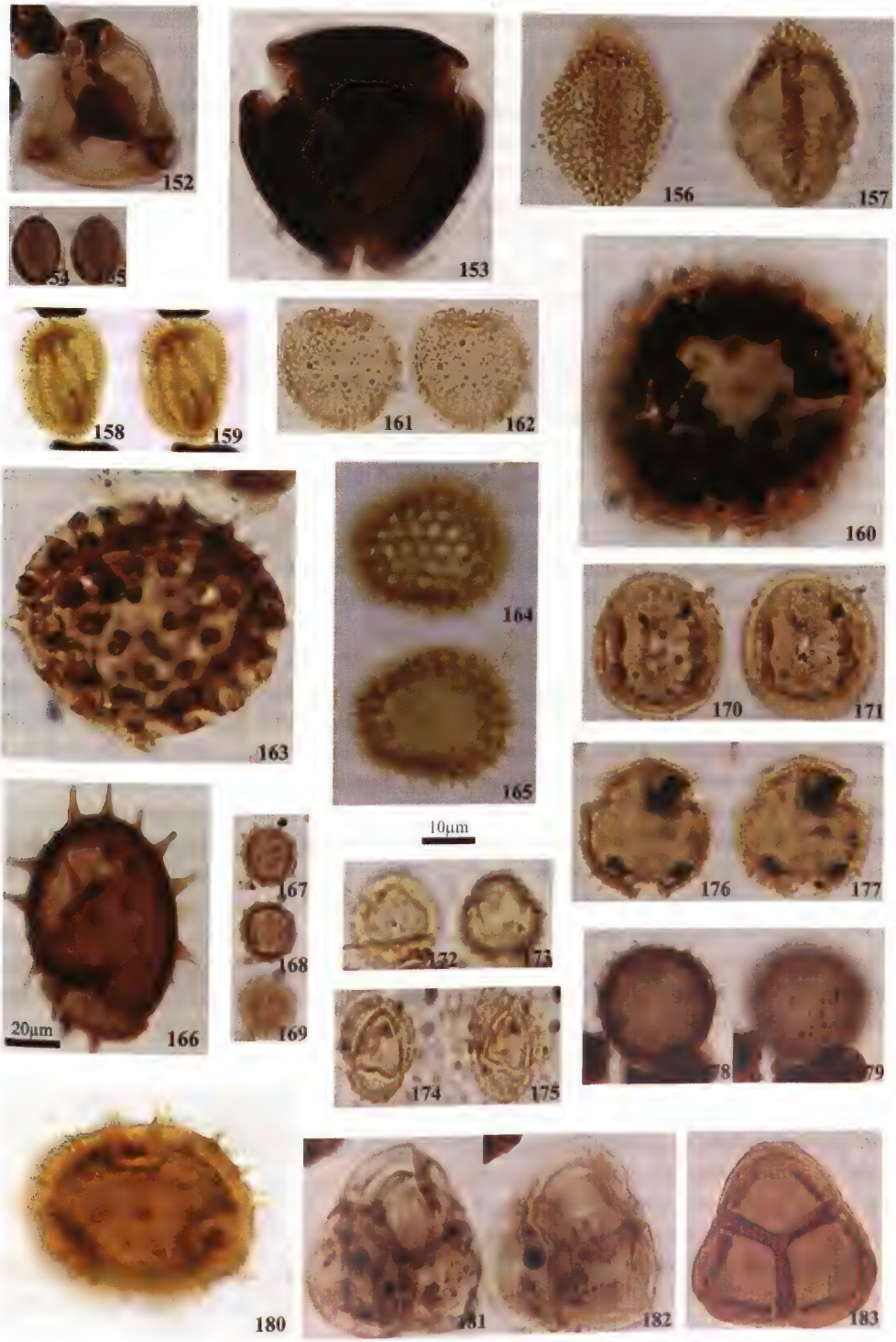
Echitricolporites spinosus (Figs. 172, 173). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, straight, wide, pores inconspicuous, apparently lalongate; echinate, echinae coarse, 1 µm long, wide at base, acute ends; tectate, wall 2.5 µm thick, sexine clearly separated from nexine; 15 µm. Ref: ID 263 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Tubiliflorae, *Espeletia* Mutis ex Bonpl., *Mikania* Willd., *Pectis* L., *Riencourtia* Cass., *Wedelia* Jacq., *Wulffia* Neck. ex Cass. types.

Echitricolporites "spinosus" var. *"microspinosus"* (Figs. 174, 175). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, pores inconspicuous; echinate, echinae thin, short, < 1 µm long, scarce, acute ends; tectate, wall 2 µm thick; 18 µm. Affinity: Dicotyledonae.

Echitricolporites "vesiculoides." Ref: ID 2094 (Jaramillo & Rueda, 2013). Ref: figs. 42, 43 (Graham, 1988a). Affinity: Dicotyledonae, Asteraceae.

Echitriporites "abutiloensis" (Figs. 176, 177). Suboblate, amb circular; triporate, pores circular, ca. 5 µm wide, bordered by dense patches of small baculae; baculate, baculae 1–2.5 µm long; intectate, wall 2.5 µm thick (excluding ornamentation);

PLATE 6. Figures 152–183.
152. *Corsinipollenites psilatus* SL 6, EF R-19/4, Gatun Fm. –9.6 Ma.
153. *Crassiectoapertites columbianus* SL 357, EF O-39/3=4, Gatun Fm. –10.05 Ma.
154, 155. *Cricotriporites* "minimus" SL 2202, EF V-33/4, Shark Hole Point Fm. –4.6 Ma.
156, 157. *Crototricolpites* "euphorbiensis" SL 307, EF S-19/3, Chagres Fm. –10.0 Ma.
158, 159. *Crototricolpites* "pseudodaemoni" SL La Boca 58.5, EF E-55, Culebra Fm. –19.24 Ma.
160. Cucurbitaceae Type SL 307, EF E-16/1, Cayo Agua Fm. –3.55 Ma.
161, 162. *Echiperiporites akanthos* SL 1617, EF U-24, Pucro Fm. –6.95 Ma.
163. *Echiperiporites estelae* SL 6, EF D-4, Gatun Fm. –9.6 Ma.
164, 165. *Echiperiporites* "ipomoensis" SL 349, EF Y-20, Cayo Agua Fm. –4.25 Ma.
166. *Echiperiporites* "pantagruelicus" SL 1152, EF Q-18, Cayo Agua Fm. –3.55 Ma.
167–169. *Echitricolporites* "chiquitinus" SL G26-1, EF L-44, Gatun Fm. –10.0 Ma.
170, 171. *Echitricolporites* "microspinosus" SL 193, EF E-22/4, Tuira Fm. –12.6 Ma.
172, 173. *Echitricolporites spinosus* SL 174, EF X-16/1, Gatun Fm. –10.2 Ma.
174, 175. *Echitricolporites* "spinosus" var. "microspinosus" SL196, EF L39/1, Cayo Agua Fm.–4.25 Ma.
176, 177. *Echitriporites* "abutiloensis" SL 177, EF R-12/4, Escudo Veraguas Fm. –2.05 Ma.
178, 179. *Echitriporites* aff. "eocenicus" SL G27-2, EF Q-14, Gatun Fm. –5.6 Ma.
180. *Echitriporites* "megaexinatus" SL Cucaracha 46.5, EF E-38/2, Cucaracha Fm. –18.48 Ma.
181, 182. *Ericipites* "baculatus" SL G26-1, EF Q-11/2, Cayo Agua Fm. –4.25 Ma.
183. *Ericipites* "psilatus" SL G27-2, EF F-20=F-21, Gatun Fm. –10.0 Ma.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10µm
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27 µm. Affinity: Dicotyledonae, Malvaceae-Malvoideae, *Abutilon* Mill.

Echitriporites aff. "*eocenicus*" (Figs. 178, 179). Suboblate, amb circular; triporate, pores circular, ca. 5 µm wide, subtly bordered by dense patches of small baculae; baculate, baculae variable, irregular, large and bottle shaped, scarce, short and thin, densely distributed; intectate, wall 2 µm thick (excluding ornamentation); 24 µm. Affinity: Dicotyledonae, Theaceae.

Echitriporites "*megaexinatus*" (Fig. 180). Subprolate, amb circular; triporate, pores circular, 4–7 µm wide, costate, annulus thick; echinate, echinae 5 µm long, scarcely distributed; tectate, wall ca. 3 µm thick; 50 µm. Affinity: Dicotyledonae.

Ericaceae Type 1. Ref: fig. 18 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 1.

Ericaceae Type 2. Ref: fig. 19 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 2.

Ericipites "*baculatus*" (Figs. 181, 182). Tetrahedral tetrad and crossed tetrad; individual grains oblate, amb circular-trilobate; tricolporate, colpi equatorially arranged, equidistant, wide, acute, 3/4 as long as grain, having thin costae, pores probably elongated-ellipsoidal; baculate, baculae as free columellae < 1 µm long; intectate, wall 1 µm thick; tetrahedral tetrad 30–33 µm, crossed tetrad 25 × 33 µm. Affinity: Dicotyledonae, Ericaceae.

Ericipites "*psilatus*" (Fig. 183). Tetrahedral tetrad; individual grains oblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, wide, rounded ends, marginate, margo coarse, pores lalongate, displaying the "H" condition, masked by point of junction between grains; psilate to slightly scabrate; tectate, wall 2 µm thick; individual grain 24 µm, tetrad 34 µm. Ref: fig. 19 (Graham, 1991b). Affinity: Dicotyledonae, Ericaceae Type 2.

Erythrina. Ref: fig. 26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Erythrina* L.

Euphorbiaceae (cf. *Glycydendron*). Ref: figs. 21, 22 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Glycydendron* Ducke.

Euphorbiaceae (cf. *Jatropha*). Ref: fig. 20 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Jatropha* L.

Euphorbiaceae (cf. *Stillingia*). Ref: fig. 23 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, cf. *Stillingia* Garden ex L.

Fagaceae (*Quercus*). Ref: fig. 16 (Graham, 1991b). Affinity: Dicotyledonae, Fagaceae, *Quercus* L.

Fenestrites spinosus (Figs. 184, 185). Spheroidal, amb circular; lophate, ca. 20 lacunae, lacunae almost pentagonal, 6 µm wide, lacunae bridges 2 µm wide; echinate, echinae short, 1–1.5 µm long, acute ends; tectate, wall 7 µm thick, strongly columellate, columellae bifurcated; 28 µm. Ref: ID 319 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Asteraceae, Liguliflorae, *Vernonia* Schreb.

Foveostephanocolpites CU488. Ref: fig. 107 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 4.

Foveotricolporites "*brevicolpatus*" (Figs. 186, 187). Spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, straight, inconspicuous; pores circular; foveolate; tectate, wall 1 µm thick; 39 × 35 µm. Affinity: Dicotyledonae.

Foveotricolporites "*cingulatum*" (Figs. 188, 189). Prolate, amb circular; tricolporate, colpi equato-

rially arranged, equidistant, extending nearly entire length of grain, straight, thin, surrounded by a thick and conspicuous margo becoming wider at equator, pore elongated almost as a continuous equatorial ring (colpus equatorialis); reticulate, lumina 1 µm wide, muri simplicolumellate; tectate, wall 1.8 µm thick; 38 × 22 µm. Affinity: Dicotyledonae, Euphorbiaceae, *Sapium caudatum* Pittier.

Foveotricolporites "*colonensis*." Ref: ID 116 (Jaramillo & Rueda, 2013). Ref: figs. 46–48 (Graham, 1988a). Affinity: Dicotyledonae, Dilleniaceae, *Doliocarpus* Rol.

Foveotriporites "*bocencis*" (Figs. 190, 191). Spherical, amb circular; triporate, pores circular, 4 µm wide; foveolate, foveolae variable, 1–1.5 µm wide; tectate, wall 2–3 µm thick; 38 µm. Ref: figs. 101, 102–104 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Types 11 & 12.

Foveotriporites "*ochromensis*" (Figs. 192, 193). Spherical, amb circular; triporate, pores circular, 6 µm wide, annulate, annulus 2.5 µm thick; foveolate, foveolae variable, 1.5–4.5 µm wide; semitectate, wall scrobiculate, 2.5 µm thick; 35 µm. Affinity: Dicotyledonae, Malvaceae–Bombacoideae, *Ochroma pyramidale* (Cav. ex Lam.) Urb.

Foveotriporites "*protohammenii*" (Fig. 194). Spherical, amb circular; triporate, pores circular, 3.5 µm wide; foveolate, foveolae 1 µm wide; tectate, wall 2 µm thick; 30 µm. Ref: figs. 63, 64 (Graham, 1988a). Affinity: Dicotyledonae, Rubiaceae, *Sabicea* Aubl.

Gemmatricolporites sp. Ref: figs. 105, 106 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 6.

Gemmatriporites "*matisialis*" (Figs. 195, 196). Spherical, amb circular; triporate, pores inconspicuous, wide, annulate, surrounded by dense gemmae; gemmate, gemmae 1.5 µm tall; intectate, wall 1 µm thick; 25 µm. Affinity: Dicotyledonae, Malvaceae-Bombacoideae.

Hauya. Ref: fig. 37 (Graham, 1991b). Affinity: Dicotyledonae, Onagraceae, *Hauya* DC.

Heterocolpites "*combretoides*" (Figs. 197–199). Spherical, amb circular-hexalobate; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, extending nearly entire length of grain, 1.5 µm wide, pores elongated; psilate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 12 µm. Affinity: Dicotyledonae, Combretaceae, *Combretum* Loefl.

Heterocolpites incomptus. Ref: ID 1021 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Melastomataceae, *Miconia* Ruiz & Pav.

Heterocolpites "*irregularis*" (Figs. 200, 201). Spherical, amb circular; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, inconspicuous, extending nearly entire length of grain, pore indistinct, circular; psilate, slightly scabrate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 9.5 µm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites "*melastomicus*" (Figs. 202, 203). Subprolate, amb circular-hexalobate; heterocolpate, with three pseudocolpi, equatorially arranged, equidistant, colpi thin, extending nearly entire length of grain, showing slightly "exitus digitus," pores circular to slightly ovate, 4 µm wide; psilate; tectate, wall 1 µm thick; 15 × 12.5 µm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites "*minutus*" (Figs. 204–206). Prolate spheroidal, amb circular; heterocolpate, with three

pseudocolpi, equatorially arranged, equidistant, colpi thin, inconspicuous, extending nearly entire length of grain, pores elongated, becoming almost rectangular, depressed, colpori wider than colpi; psilate; tectate, wall 1 µm thick; 9 × 8 µm. Affinity: Dicotyledonae, Melastomataceae.

Heterocolpites rotundus. Ref: ID 1022 (Jaramillo & Rueda, 2013); figs. 4, 5 (Graham, 1991b); figs. 40, 41 (Graham, 1988a). Affinity: Dicotyledonae, Combretaceae, *Combretum/Terminalia* L. types.

Ilexpollenites "clavavariatus." Ref: ID 2093 (Jaramillo & Rueda, 2013); fig. 3 (Graham, 1991a). Affinity: Dicotyledonae, Aquifoliaceae, *Ilex* L.

Ilexpollenites "larguitus" (Figs. 207, 208). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 3/4 length of grain, slightly irregular, margins masked by sculptural elements, pore inconspicuous, apparently circular; clavate, clavae irregular, < 1 to 2.5 µm high; intectate, wall ca. 1 µm thick; 30 × 23 µm. Affinity: Dicotyledonae, Aquifoliaceae, *Ilex*.

Inaperturopollenites "crotonoides" (Figs. 209, 210). Spherical, amb circular; inaperturate; clavate, clavae arranged in a crotonoid pattern; intectate, wall 1.5 µm thick; 23 µm. Affinity: Dicotyledonae.

Inaperturopollenites "grandiosus" (Fig. 211). Spherical, amb circular; inaperturate; gemmate, gemmae ca. 1 µm tall, rounded, uniformly distributed; intectate, wall 2.5 µm thick; 122 µm. Affinity: Dicotyledonae, Annonaceae.

Inaperturopollenites "reticulatus" (Figs. 212, 213). Spherical, amb circular; inaperturate; reticulate, lumina variable, muri coarse, simplicolumellate, columellae clavate-shaped, ca. 1.5 µm long, rounded; tectate, tectum subtle, wall 2.5 µm thick; 19 µm. Ref: fig. 40 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Chomelia* Jacq. type.

Ladakhipollenites simplex. Ref: ID 424 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Lanagiopollis crassa (Fig. 214). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 2/3 length of grain, costate,

PLATE 7. Figures 184–221.
184, 185. *Fenestrites spinosus* SL 175, EF Q-6/4, Escudo Veraguas Fm. –2.05 Ma.
186, 187. *Foveotricolporites* "brevicolpatus" SL Culebra 1.5, EFG-54/1, Culebra Fm. –19.18 Ma.
188, 189. *Foveotricolporites* "cingulatum" SL 178, EF Q-22/3, Tuira Fm. –12.6 Ma.
190, 191. *Foveotriporites* "bocencis" SL La Boca 67.5, EF H-45/3, Culebra Fm. –19.20 Ma.
192, 193. *Foveotriporites* "ochromensis" SL 1997, EF X-38/1, Chucunaque Fm. –6.95 Ma.
194. *Foveotriporites* "protohammenii" SL Culebra 3.5, EF V-18/4, Culebra Fm. –19.11 Ma.
195, 196. *Gemmatriporites* "matisialis" SL 18, EF J-24/1, Gatun Fm. –5.6 Ma.
197–199. *Heterocolpites* "combretoides" SL G26-1, EF N-23/3, Gatun Fm. –10.0 Ma.
200, 201. *Heterocolpites* "irregularis" SL 174, EF G-33/1, Escudo Veraguas Fm. –2.05 Ma.
202, 203. *Heterocolpites* "melastomicus" SL G26-1, EF H-17/3, Tuira Fm. –6.95 Ma.
204–206. *Heterocolpites* "minutus" SL 174, EF E-48/4, Escudo Veraguas Fm. –3.55 Ma.
207, 208. *Ilexpollenites* "larguitus" SL G26-1, EF R-8, Tuira Fm. –12.6 Ma.
209, 210. *Inaperturopollenites* "crotonoides" SL 11, EF G-7/4, Escudo Veraguas Fm. –2.75 Ma.
211. *Inaperturopollenites* "grandiosus" SL 19, EF O-19/4, Gatun Fm. –5.6 Ma.
212, 213. *Inaperturopollenites* "reticulatus" SL G27-2, EF C-6, Gatun Fm. –10.2 Ma.
214. *Lanagiopollis crassa* SL 178, EF S-7/4, Tuira Fm. –12.6 Ma.
215. *Loranthaceae* "atriensis" SL 11, EF J-10, Gatun Fm. –5.6 Ma.
216, 217. *Loranthaceae* "marginalis" SL 168, EF D-17/1, Nancy Point Fm. –5.65 Ma.
218, 219. *Loranthaceae* "oryctanthusis" SL 175, EF F-51/4, Escudo Veraguas Fm. –2.05 Ma.
220, 221. *Malpighiaceae* "bunchoensis" SL 174, EF M-25/1; SL 391, EF K-10/4, Gatun Fm. –9.6 Ma.

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straight, wide, pore lalongate, ca. 7 × 23 µm; reticulate, lumina < 1 µm wide. Muri thin, pluricolumellate, columellae densely present, thin; tectate, wall 3–3.5 µm thick; 41–57 µm. Ref: ID 430 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Leguminosae. Ref: figs. 24–26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae.

Lentibulariaceae. Ref: fig. 30 (Graham, 1991b). Affinity: Dicotyledonae, Lentibulariaceae, *Utricularia* L.

Loranthaceae "*atriensis*" (Fig. 215). Oblate, amb triangular-obtuse-concave; syncolpate, colpus thin; psilate to scabrate; tectate, wall thickest at intercolpium; 27 µm. Affinity: Dicotyledonae, Loranthaceae.

Loranthaceae "*marginalis*" (Figs. 216, 217). Oblate, amb triangular-obtuse-concave; syncolpate, colpi joined at polar areas forming small triangle (para-syncolpate condition), surrounded by thick and conspicuous margo; psilate; tectate, wall < 0.5 µm thick at intercolpium areas and 1 µm thick at aperture areas; 22 µm. Affinity: Dicotyledonae, Loranthaceae.

Loranthaceae "*oryctanthusis*" (Figs. 218, 219). Oblate, amb circular-semitriangular; tricolpate, structure complex, colpi joined at polar areas, bifurcated, forming three circular plates (aspis?) probably with pseudopori, each one 6 µm wide; psilate; tectate, wall 1 µm thick; 26 µm. Affinity: Dicotyledonae, Loranthaceae, *Oryctanthus* (Griseb.) Eichler.

Loranthaceae Type 1. Ref: fig. 31 (Graham, 1991b). Affinity: Dicotyledonae, Loranthaceae Type 1.

Loranthaceae Type 2. Ref: fig. 32 (Graham, 1991b). Affinity: Dicotyledonae, Loranthaceae Type 2.

Malpighiaceae "*bunchoensis*" (Figs. 220, 221). Spherical, amb circular; periporate, 4 to 6 pores, equidistant, pores circular, 4–5 µm wide; psilate; tectate, wall 1 µm thick, tectum 0.5 µm thick, sexine 0.5 µm thick, nexine 0.5 µm thick; 22 µm. Affinity: Dicotyledonae, Malpighiaceae.

Malpighiaceae Type 2. Ref: fig. 40 (Graham, 1989); fig. 33 (Graham, 1991b). Affinity: Dicotyledonae, Malpighiaceae Type 2.

Margocolporites "*hematoxyformis*" (Figs. 222, 223). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, wide, acute ends, pores circular, 5 µm wide, annulate; reticulate, muri simplicolumellate, lumina variable, 1.5 µm wide; tectate, wall 2 µm thick; 22 µm. Affinity: Dicotyledonae, Fabaceae–Caesalpinioideae, *Caesalpinia* L.

Margocolporites vanwijhei. Ref: ID 465 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Fabaceae, *Adipera* Raf., *Brasilettia* (DC.) Kuntze, *Haematoxylum* L., *Mezoneuron* Desf., *Poincianella* Britton & Rose, *Caesalpinia bonduc* (L.) Roxb., *C. coriaria* (Jacq.) Willd.

Melastomataceae. Ref: fig. 27 (Graham, 1991b). Affinity: Dicotyledonae, Melastomataceae.

Momipites africanus (Figs. 224, 225). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, 2.5 µm wide, subtly protruding, annulate, annulus thin; psilate to slightly scabrate; tectate, wall 1 µm thick; 23 µm. Ref: ID 478 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Betulaceae, *Corylus* L.

Momipites "*panamensis*." Ref: ID 2097 (Jaramillo & Rueda, 2013); fig. 30 (Graham, 1988b); fig. 33 (Graham, 1989); fig. 17 (Graham, 1991b). Affinity: Dicotyledonae, Juglandaceae, *Alfaroa* Standl./*Oreomunnea* Oerst., *Alfaroa*/*Engelhardia* Lesch. ex Blume types.

Multimarginites vanderhammenii. Ref: ID 492 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Acanthaceae, *Sanchezia klugii* Leonard & L. B. Sm.

Myrtaceae Type (Figs. 226, 227). Oblate, amb triangular-acute-straight; syncolporate, colpi equatorially arranged, equidistant, straight, thin, pores circular, ca. 1.5 µm wide; psilate to slightly scabrate; tectate, wall < 1 µm thick; 20 µm. Affinity: Dicotyledonae, Myrtaceae, *Psidium* L.

Nymphaeaceae. Ref: fig. 38 (Graham, 1991b). Affinity: Dicotyledonae, Nymphaeaceae, *Cabomba*.

Ochnaceae Type (Figs. 228, 229). Suboblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, thin, inconspicuous, short, marginate, margo coarse, pores circular, 3 µm wide, annulate; reticulate, lumina homogeneous, fine, < 1 µm wide, muri thin, simplicolumellate; tectate, wall 1 µm thick; 16.5 × 18 µm. Affinity: Dicotyledonae, Ochnaceae.

Onagraceae. Ref: fig. 37 (Graham, 1991b). Affinity: Dicotyledonae, Onagraceae, *Hauya*.

Pachydermites diederixi (Fig. 230). Suboblate to spheroidal, amb circular; stephanoporate, pores equatorially arranged, equidistant, circular, 6 µm wide, margins irregular; psilate; tectate, wall 4.5–5 µm thick; 42 µm. Ref: ID 509 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Clusiaceae, *Symphonia globulifera* L. f.

Papilionoideae. Ref: fig. 26 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Faboideae, *Erythrina* L.

Parsonsidites "*multiporatus*" (Figs. 231, 232). Spherical, amb circular; periporate, 5 pores, circular, 3 µm wide, annulate; psilate; tectate, wall 1 µm thick; 17 µm. Affinity: Dicotyledonae.

Perisyncolporites "*gemmatus*" (Figs. 233, 234). Spherical, amb circular; perisyncolporate, pseudocolpi inconspicuous, gemmate, gemmae 3 × 2–4 µm, ends rounded, pores circular; semitectate, wall 8 µm thick, columellae 1 µm tall, tectum 3 µm thick, tectum restricted only beneath gemmae; 25 µm. Affinity: Dicotyledonae, Malpighiaceae.

Perisyncolporites pokornyi (Figs. 235, 236). Spherical, amb circular; periporate, sometimes having subtle pseudocolpi resembling the perisyncolporate condition, pores circular, 3.5 µm wide; psilate; tectate, wall 3 µm thick, columellate, columellae baculae-shaped; 27 µm. Ref: ID 532 (Jaramillo & Rueda, 2013); figs. 61, 62 (Graham, 1988a). Affinity: Dicotyledonae, Malpighiaceae, *Brachypterys* A. Juss., *Banisteroides*, *Bunchosia* Rich. ex Juss., *Hiraea* Bertero ex DC., *Mascagnia* (Bertero ex DC.) Bertero, *Stigmaphyllon* A. Juss., *Tetrapterys* Cav.

Poloretitricolpites "*centenarius*." Ref: figs. 78, 79 (Graham, 1988a). Affinity: Dicotyledonae, Sapotaceae, *Pouteria* Aubl.

Polyadopollenites mariae (Fig. 237). Sixteen-celled polyad; individual grains oblate, amb trapezoid; probably periporate, pores small, inconspicuous, restricted to point of junction of grain; psilate; tectate, wall 2.5 µm thick, thicker at distal face; individual grains ca. 18 µm, polyad 45 µm. Ref: fig. 24 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae–Mimosoideae, *Acacia* Mill.

Polyadopollenites "*minutus*" (Figs. 238, 239). Sixteen-celled polyad; individual grains oblate, amb square to polygonal; periporate, pores small, circular; scabrate; tectate, wall 1 µm thick; individual grains ca. 10 µm, polyad 27 × 21 µm. Affinity: Dicotyledonae, Fabaceae–Mimosoideae, *Acacia*.

Pouteria "*mamey*" (Figs. 240, 241). Subprolate, amb circular; tricolporate, colpi equatorially ar-

ranged, equidistant, short, thin, half as long as grain, pores appearing circular, small; psilate; tectate, wall 1.5 µm thick; 20 × 18 µm. Affinity: Dicotyledonae, Sapotaceae, *Pouteria*.

Proteacidites triangulatus (Figs. 242, 243). Suboblate, amb triangular; triporate, pores equatorially arranged, equidistant, circular, 3.5 µm wide; reticulate, sometimes appearing as psilate, lumina very fine, < 0.5 µm wide, muri thin, strongly columellate; tectate, wall 1 µm thick; 22 µm. Ref: ID 562 (Jaramillo & Rueda, 2013): fig. 57 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Allophylus* L.

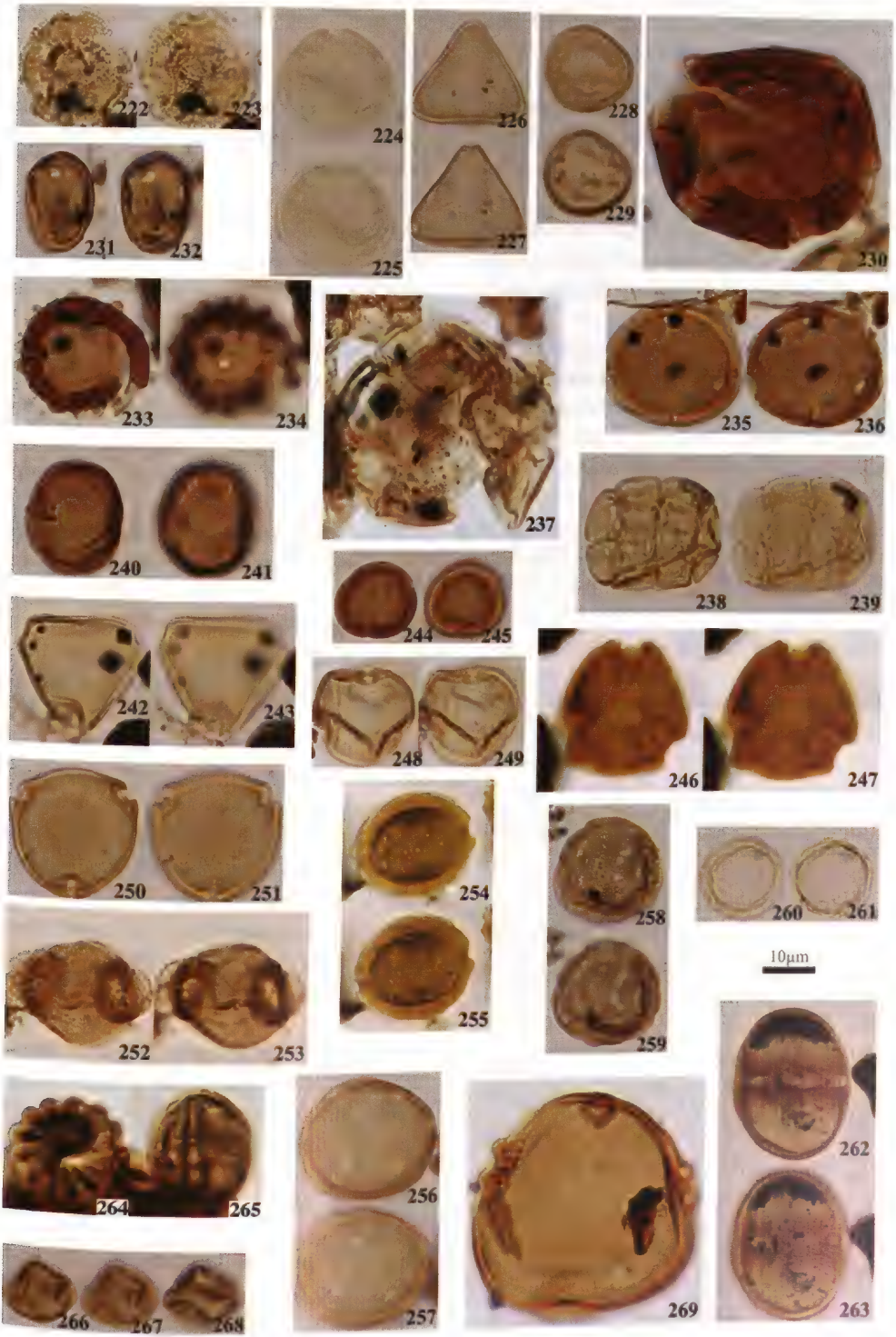
Psilabrevitricolpites aff. *flexibilis* (Figs. 244, 245). Subprolate, amb circular; tricolporate (although originally it was described as tricolpate), colpi equatorially arranged, equidistant, short, extending half the length of the grain, thin, acute ends, pores inconspicuous, apparently circular, small; psilate, sometimes resembling micropitted pattern; tectate, wall 2 µm thick; 15 µm. Ref: ID 580 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Psilabrevitricolporites devriesi. Ref: ID 637 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Humiriaceae, *Humiria* Aubl.

Psilabrevitricolporites "*magnoporatus*" (Figs. 246, 247). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, wide, pores inconspicuous, apparently circular, annulate; psilate; tectate, wall ca. 2 µm thick; 26 µm. Affinity: Dicotyledonae.

Psilabrevitricolporites aff. *rotundus* (Figs. 248, 249). Spherical, amb circular; tricolporate, sometimes appearing as triporate, colpi equatorially arranged, equidistant, subtle, very thin, inconspicuous, pores circular, 1 µm wide, annulate, annulus coarse; psilate; tectate, wall 1 µm thick; 18 µm. Affinity: Dicotyledonae.

PLATE 8. Figures 222–269.
222, 223. *Margocolporites* "hematoxyformis" SL 193, EF W-12/4, Gatun Fm. –5.6 Ma.
224, 225. *Momipites africanus* SL 174, EF D-9/4, Gatun Fm. –9.6 Ma.
226, 227. Myrtaceae Type SL 177, EF E-9/4, Gatun Fm. –9.6 Ma.
228, 229. Ochnaceae Type SL G27-2, EF E-5, Gatun Fm. –9.6 Ma.
230. *Pachydermites diederixi* SL 174, EF K-8/2, Chagres Fm. –10.0 Ma.
231, 232. *Parsonsidites* "multiporatus" SL 2174, EF V-15, Chagres Fm. –10.0 Ma.
233, 234. *Perisyncolporites* "gemmatus" SL 307, EF O-10/4, Gatun Fm. –8.9 Ma.
235, 236. *Perisyncolporites pokornyi* SL 174, EF E-22/4=E-23/3, Tuira Fm. –12.6 Ma.
237. *Polyadopollenites mariae* SL 193, EF Y-17/1=3, Tuira Fm. –6.95 Ma.
238, 239. *Polyadopollenites* "minutus" SL 176, EF C-21/3, Escudo Veraguas Fm. –2.05 Ma.
240, 241. *Pouteria* "mamey" SL G26-1, EF H-12/3, Gatun Fm. –5.6 Ma.
242, 243. *Proteacidites triangulatus* SL 178, EF M-7/4, Pucro Fm. –6.95 Ma.
244, 245. *Psilabrevitricolpites* aff. *flexibilis* SL 178, EF A-23/3, Tuira Fm. –12.6 Ma.
246, 247. *Psilabrevitricolporites* "magnoporatus" SL Culebra 15, EF X-21/2, Culebra Fm. –19.15 Ma.
248, 249. *Psilabrevitricolporites* aff. *rotundus* SL G27-2, EF E-26/2=4, Tuira Fm. –6.95 Ma.
250, 251. *Psilabrevitricolporites* "vestibulatus" SL 350, EF T-16/4, Lara Fm. –6.95 Ma.
252, 253. *Psiladiporites* "faramensis" SL 1617, EF P-18/2=4, Chucunaque Fm. –6.95 Ma.
254, 255. *Psiladiporites* "infragranulatus" SL Culebra 19, EF J-43/2, Culebra Fm. –19.1 Ma.
256, 257. *Psilaperiporites* "juglands" SL 888, EF J-9/4, Chucunaque Fm. –7.05 Ma.
258, 259. *Psilaperiporites minimus* SL 1253, EF F-44/3=4, Chagres Fm. –10.0 Ma.
260, 261. *Psilastephanocolporites* "acalyphoides" SL 176, EF Q-20/4, Cayo Agua Fm. –4.25 Ma.
262, 263. *Psilastephanocolporites* "cedreloides" SL 5a, EF M-16/1, Gatun Fm. –5.6 Ma.
264, 265. *Psilastephanocolporites fissilis* SL 307, EF D-16/4, Cayo Agua Fm. –3.55 Ma.
266–268. *Psilastephanoporites* "crassiannulatus" SL G27-1, EF K-14/4, Tuira Fm. –6.95 Ma.
269. *Psilastephanoporites herngrenii* SL 1142, EF Q-8/2, Tuira Fm. –6.95 Ma.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Psilabrevitricolporites triangularis. Ref: ID 588 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapindaceae?

Psilabrevitricolporites "vestibulatus" (Figs. 250, 251). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, pores 3.5 µm wide, vestibulate, apparently annulate; psilate; tectate, wall 2–3.5 µm thick, thickness around pores; 23 µm. Affinity: Dicotyledonae.

Psiladiporites "faramensis" (Figs. 252, 253). Oblate, amb ellipsoidal; diporate, pores annulate, protruding, covered by thin membrane, circular, 4 µm wide, annulus 3.5 µm thick; psilate; tectate, wall < 1 µm thick; 19 × 27 µm. Affinity: Dicotyledonae, Rubiaceae, *Faramea* Aubl.

Psiladiporites "infragranulatus" (Figs. 254, 255). Oblate, amb ellipsoidal; diporate, pores circular, 3.5 µm wide; psilate; tectate, wall ca. 2 µm thick; 19 × 25 µm. Affinity: Dicotyledonae.

Psilaperiporites "juglands" (Figs. 256, 257). Spheroidal, amb circular; periporate, ca. 13 pores, pores slightly protruding, circular, 2.5 µm wide, annulate, annulus 1 × 4 µm; psilate; tectate, wall 2 µm thick; 27 µm. Affinity: Dicotyledonae, Juglandaceae, *Juglans* L.

Psilaperiporites minimus (Figs. 258, 259). Spheroidal, amb circular; periporate, > 40 pores, pores circular, 1µm wide, irregularly distributed; scabrate, resembling punctate pattern; tectate, wall 1.2 µm thick, strongly columellate; 21 µm. Ref: ID 594 (Jaramillo & Rueda, 2013); fig. 39 (Graham, 1988a). Affinity: Dicotyledonae, Chenopodiaceae/Amaranthaceae.

Psilastephanocolpites "janduforius." Ref: figs. 94, 95 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 5.

Psilastephanocolporites "acalyphoides" (Figs. 260, 261). Spherical, amb circular; stephanocolporate, apertures 5, colpi equatorially arranged, equidistant, inconspicuous, short, thin, pores small, circular, slighty protuberant; psilate to almost verrucate; tectate, wall ca. 1 µm thick; 15 µm. Affinity: Dicotyledonae, Euphorbiaceae, *Acalypha diversifolia* Jacq.

Psilastephanocolporites "cedreloides" (Figs. 262, 263). Prolate spheroidal, amb circular; stephanocolporate, apertures 5, colpi equatorially arranged, equidistant, extending 3/4 length of grain, ca. 35 × 5 µm, having a continuous equatorial costa, pores ellipsoidally lalongate, almost joining, resembling a zonorate ring; psilate; tectate, wall ca. 1.5 µm thick; 28 × 24 µm. Ref: fig. 35 (Graham, 1991b). Affinity: Dicotyledonae, Meliaceae, *Cedrela* P. Browne.

Psilastephanocolporites fissilis (Figs. 264, 265). Prolate-spheroidal to spheroidal, amb circular; stephanocolporate, apertures 13, colpi equatorially arranged, equidistant, extending nearly entire length of grain, thin, having a continuous equatorial costa, pores lalongate, almost joining, resembling a zonorate ring; psilate; tectate, wall ca. 2.5 µm thick; 23 × 21 µm. Ref: ID 604 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Polygalaceae, *Polygala* L.

Psilastephanoporites "crassiannulatus" (Figs. 266–268). Spherical, amb circular; stephanoporate, 4 pores, pores equatorially arranged, costate, costae 1.5 µm thick; psilate; tectate, wall 1.5 µm thick; 13 µm. Affinity: Dicotyledonae.

Psilastephanoporites herngrenii (Fig. 269). Oblate, amb circular; stephanoporate, apertures 4, pores equatorially arranged, circular, 3 µm wide, annulate, annulus 3.5 µm thick; psilate; tectate, wall ca. 1.8 µm thick; 44 µm. Ref: ID 1019 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Apocynaceae.

Psilastephanoporites "magnus" (Fig. 270). Spherical, amb circular; stephanoporate, pores protruding,

annulate, costate, wide; psilate; tectate, wall 2.5 µm thick, tectum clearly differentiated from nexine; 71 µm. Affinity: Dicotyledonae, Apocynaceae.

Psilastephanoporites "microcaribiensis" (Figs. 271, 272). Spherical, amb circular; stephanoporate, pores 4, simple, circular, ca. 3 µm wide; psilate; tectate, wall 1 µm thick; 19 µm. Affinity: Dicotyledonae.

Psilastephanoporites "punctatus" (Fig. 273). Spherical, amb circular; stephanoporate, 4 pores, circular, 4 µm wide, costate, annulus thick; psilate; intectate; wall 1.5 µm thick; 30 µm. Affinity: Dicotyledonae.

Psilasyncolpites "recticolpatus" (Figs. 274, 275). Oblate, amb triangular-obtuse-straight; syncolpate, colpi continuous, joining at apices; psilate; tectate, wall 1 µm thick, decreasing toward polar areas; 23 µm. Affinity: Dicotyledonae, Myrtaceae.

Psilasyncolporites "reticolpatus" (Figs. 276, 277). Oblate, amb triangular-obtuse slightly concave; apparently syncolporate, colpi continuous, joining at apices, forming a small triangle (parasyncolporate condition), pore, if present, inconspicuous; psilate; tectate, wall 1 µm thick; 22 µm. Affinity: Dicotyledonae, Loranthaceae, *Struthanthus* Mart.

Psilatricolpites CU490. Ref: figs. 82–86 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 2.

Psilatricolporites "communis" (Figs. 278, 279). Oblate spheroidal, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, acute ends, pore apparently circular, becoming elongated, protruding; tectate, wall 1 µm thick; 16.5 × 18 µm. Affinity: Dicotyledonae.

Psilatricolporites costatus. Ref: ID 635 (Jaramillo & Rueda, 2013); fig. 53 (Graham, 1988a). Affinity: Dicotyledonae, Salicaceae, *Casearia* Jacq.

Psilatricolporites "crassiexinatus" (Figs. 280, 281). Suboblate, amb circular trilobate; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore elongated; psilate; tectate, wall 5 µm thick; 41 µm. Affinity: Dicotyledonae.

Psilatricolporites "faboides" (Figs. 282, 283). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending 3/4 length of grain, thin, pores elongated, becoming circular, 3.5 µm; psilate; tectate, wall 1 µm thick; 14 × 12.5 µm. Affinity: Dicotyledonae, Fabaceae–Faboideae.

Psilatricolporites "hornii" (Fig. 284). Suboblate, amb circular; tricolpate, colpi equatorially arranged, equidistant, short, marginate, margo very thick, prominent; psilate; tectate, wall < 0.5 µm thick; 29 × 32 µm. Affinity: Dicotyledonae, Apocynaceae.

Psilatricolporites "rotund" (Fig. 285). Subprolate, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, costate, pores lalongate; psilate, apparently microreticulate; tectate, wall 1 µm thick, displaying short columellae; 44.5 × 35.5 µm. Affinity: Dicotyledonae.

Psilatricolporites "sphericus" (Figs. 286, 287). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, extending nearly entire length of grain, pores circular, wide; psilate; tectate, wall 1 µm thick; 15 µm. Affinity: Dicotyledonae.

Psilatricolporites "vest" (Fig. 288). Suboblate, amb circular; tricolporate, colpi equatorially arranged, equidistant, short, costate, margo thick; psilate; tectate, wall 1 µm thick; 25 × 25 µm. Affinity: Dicotyledonae.

Psilatricolporites sp. Ref: ID 2385 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Psilatriporites "lobatus" (Figs. 289, 290). Spherical, amb triangular-obtuse-convex; triporate, pores circular, 10 µm wide, annulate, annulus 5 µm thick; psilate; tectate, wall 1.2 µm thick; 31 µm. Affinity: Dicotyledonae.

Psilatriporites "moraceoides" (Figs. 291, 292). Spherical, amb circular; triporate, pores circular, 1 µm wide, simple; psilate, slightly scabrate; tectate, wall 1.2 µm thick; 17 µm. Affinity: Dicotyledonae.

Psilatriporites "ulmoides" (Figs. 293, 294). Spherical, amb circular; triporate, pores circular, 3 µm wide, having subtle costae; psilate; tectate, wall 1.2 µm thick; 18 µm. Affinity: Dicotyledonae.

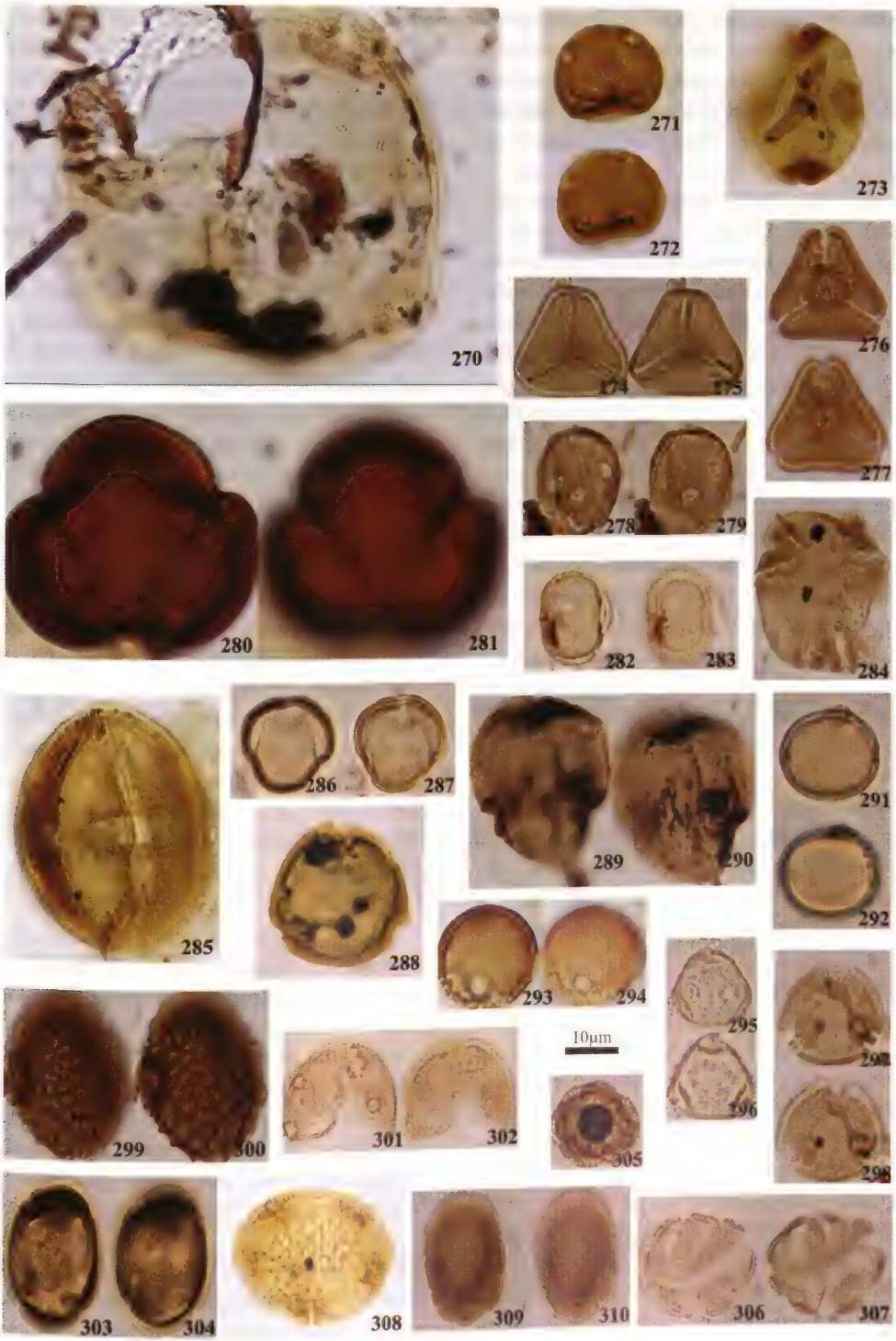
Psilatriporites "vestibulatum" (Figs. 295, 296). Spherical, amb triangular-rounded; triporate, pores circular-globose; psilate; tectate, wall < 1 µm at interporium area, 3 µm thick at apertural area; 15 µm. Affinity: Dicotyledonae.

Ranunculacidites operculatus (Figs. 297, 298). Spherical, amb circular; tricolporate, colpi equatorially arranged, equidistant, wide, short, acute ends, polar area distance between adjacent colpi 6 µm long, pores masked by conspicuous opercula, operculum thin, long, bifurcated; reticulate, lumina < 1 µm wide, muri very thin, simplicolumellate; tectate; 18 µm. Ref: ID 656 (Jaramillo & Rueda, 2013); fig. 29 (Graham, 1988b); fig. 32 (Graham, 1989); fig. 13 (Graham, 1991b). Affinity: Dicotyledonae, Euphorbiaceae, *Alchornea* Sw.

Retidiporites "cordiaeformis" (Figs. 299, 300). Spherical, amb circular; diporate, pores circular, 12 µm wide, protruding, annulate; reticulate, lumina decreasing toward center of grain; tectate, wall variable, ca. 1.5 thick; 32 µm. Affinity: Dicotyledonae.

Retipericolporites sp. (Figs. 301, 302). Spherical, amb circular; stephanocolpate, ca. 8 to 9 colpori,

PLATE 9. Figures 270–310.
270. *Psilastephanoporites* "magnus" SL 18, EF G-43/1, Gatun Fm. –5.6 Ma.
271, 272. *Psilastephanoporites* "microcaribiensis" SL Culebra 10.5, EF O-39/2, Culebra Fm. –19.4 Ma.
273. *Psilastephanoporites* "punctatus" SL Culebra 1.5, EF U-54/3, Culebra Fm. –19.46 Ma.
274, 275. *Psilasyncolpites* "recticolpatus" SL 177, EF G-6/4, Gatun Fm. –10.2 Ma.
276, 277. *Psilasyncolporites* "reticolpatus" SL 1188, EF J-25/3, Cayo Agua Fm. –4.25 Ma.
278, 279. *Psilatricolporites* "communis" SL 174, EF W-35/1, Gatun Fm. –10.05 Ma.
280, 281. *Psilatricolporites* "crassiexinatus" SL 168, EF K-10/1, Gatun Fm. –5.6 Ma.
282, 283. *Psilatricolporites* "faboides" SL 2165, EF N-6/2, Gatun Fm. –10.2 Ma.
284. *Psilatricolporites* "hornii" SLG23-1, EF K-20/1, Gatun Fm. –10.2 Ma.
285. *Psilatricolporites* "rotund" SL La Boca 27, EF X-14/4, Culebra Fm. –19.38 Ma.
286, 287. *Psilatricolporites* "sphericus" SL 2165, EF M-40/2, Gatun Fm. –9.6 Ma.
288. *Psilatricolporites* "vest" SL La Boca 27, EF U-46/3=4, La Boca Fm. –19.46 Ma.
289, 290. *Psilatriporites* "lobatus" SL 2222, EF M-43, Cayo Agua Fm. –4.25 Ma.
291, 292. *Psilatriporites* "moraceoides" SL 2165, EF N-6/4, Tuira Fm. –6.95 Ma.
293, 294. *Psilatriporites* "ulmoides" SL 207, EF L-15/4, Gatun F. –5.6 Ma.
295, 296. *Psilatriporites* "vestibulatum" SL G28-2, EF T-11, Gatun Fm. –5.6 Ma.
297, 298. *Ranunculacidites operculatus* SL 184, EF G-50/4, Gatun Fm. –10.2 Ma.
299, 300. *Retidiporites* "cordiaeformis" SL 2167, EF V-13/1, Gatun Fm. –9.6 Ma.
301, 302. *Retipericolporites* sp. SL 1566, EF O-6/2=4, Tuira Fm. –6.95 Ma.
303, 304. *Retistephanocolpites* "brevicolpatus" SL 370, EF R-68/1, Gatun Fm. –8.9 Ma.
305. *Retistephanocolpites* "hexalabiatus" SL 5a, EF S-25/3, Gatun Fm. –5.6 Ma.
306, 307. *Retistephanocolpites* "octolabiatus" SL 68, EF D-15/4, Gatun Fm. –9.6 Ma.
308. *Retistephanocolporites* "bombacoides" SL La Boca 8.5, EF K-54, Culebra Fm. –19.46 Ma.
309, 310. *Retistephanocolporites* "borrerioides" SL 1241, EF S-19, Gatun Fm. –8.9 Ma.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colpus very short, thin, lineal, apparently marginate, inconspicuous, pores circular, 1–1.5 µm wide; reticulate, lumina thin, homogeneous, muri simplicolumellate, columellae 0.5 µm long; tectate, wall 1 µm thick; 21 µm. Affinity: Dicotyledonae.

Retistephanocolpites "*brevicolpatus*" (Figs. 303, 304). Spherical, amb circular; stephanocolpate, 4 colpi, colpus equatorially arranged, equidistant, short, acute ends, polar area ample; reticulate, lumina 0.5 µm wide, muri 0.5 µm thick; tectate, wall 1.5 µm thick; 24 µm. Affinity: Dicotyledonae.

Retistephanocolpites "*hexalabiatus*" (Fig. 305). Spherical, amb circular hexalobate; stephanocolpate, 6 colpi, colpus equatorially arranged, equidistant, short, not well defined, pores probably present, inconspicuous; reticulate, lumina 1 µm wide, muri thin, simplibaculate; tectate, wall 1–2 µm thick, increasing toward intercolpium areas; 17 µm. Affinity: Dicotyledonae, Labiatae.

Retistephanocolpites "*octolabiatus*" (Figs. 306, 307). Spherical, amb circular to slightly ovate, octolobate; stephanocolpate, 8 colpi, colpus equatorially arranged, equidistant, extending nearly entire length of grain, deep, wide; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae dense; tectate, wall 1.8 µm thick; 22 × 19 µm. Affinity: Dicotyledonae, Labiatae.

Retistephanocolporites "*bombacoides*" (Fig. 308). Oblate, amb circular; stephanocolporate, 5 colpori, colpus equatorially arranged, equidistant, short, margins straight, ends pointed, pores indistinct, costate, annulus thick; reticulate-fossulate, lumina variable, 1–4 µm wide; semitectate, wall 1.5 µm thick; 30 µm. Affinity: Dicotyledonae.

Retistephanocolporites "*borrerioides*" (Figs. 309, 310). Oblate spheroidal, amb circular; stephanocolporate, 11 colpi, colpus equatorially arranged, equidistant, short, narrow, pores simple, inconspicuous; baculate, baculae 0.8 µm tall, densely distributed; intectate, wall 2 µm thick; 23 × 25 µm. Affinity: Dicotyledonae, Rubiaceae, *Borreria* G. Mey.

Retistephanoporites aff. *crassiannulatus* (Figs. 311, 312). Spherical, amb circular; stephanoporate, sometimes displaying triporate condition, pores circular, 6 µm wide, costate, annulus 2 µm thick, surrounded by coarse baculae processes; foveolate, foveolae regularly distributed, resembling reticulate pattern, 2.5 µm wide; tectate, wall 2.5 µm thick; 35 µm. Ref: ID 703 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Malvaceae-Bombacoideae, *Quararibea* Aubl.

Retitrescolpites "*amanoensis*" (Fig. 313). Spherical, amb circular-trilobate; tricolporate, colpus equatorially arranged, equidistant, extending 3/4 length of grain, rounded ends, pores probably circular, wide, inconspicuous; reticulate, lumina variable, 4–7 µm wide, having free baculae, muri 1 µm thick, simplicolumellate, undulating, irregular; semitectate, wall 5 µm thick; 41 µm. Affinity: Dicotyledonae, Phyllanthaceae, *Amanoa* Aubl.

Retitrescolpites? irregularis. Ref: ID 712 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Phyllanthaceae, *Amanoa* type, *Amanoa oblongifolia* Müll. Arg., *Pseudolachnostylis glauca* (Hiern) Hutch.

Retitrescolpites "*usualis*" (Figs. 314, 315). Subprolate, amb tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores lalongate, 2 µm long; reticulate, lumina irregular, variable, 1.5–2.5 µm wide, muri thin, < 1 µm thick, simplicolumellate, columellae 1 µm long, baculae-shaped; tectate, wall 1.8–2 µm thick; 19 × 15 µm. Affinity: Dicotyledonae.

Retitricolpites "*generalis*" (Figs. 316, 317). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, simple; reticulate,

lumina 0.7–1 µm wide; tectate, wall 1 µm thick; 34 × 29 µm. Affinity: Dicotyledonae.

Retitricolpites "*pseudosimplex*" (Figs. 318, 319). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, simple, thin; reticulate, lumina ca. 0.5 µm wide; tectate, wall 1 µm thick; 36 × 20 µm. Affinity: Dicotyledonae.

Retitricolpites simplex. Ref: ID 746 (Jaramillo & Rueda, 2013); figs. 49, 50 (Graham, 1988a). Affinity: Dicotyledonae, Euphorbiaceae, *Sapium* Jacq.

Retitricolpites "*spiraloides*." Ref: fig. 92 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 14.

Retitricolpites sp. Ref: ID 993 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, *Retitricolpites* sp. A.

Retitricolporites "*amplibrochatus*" (Figs. 320, 321). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, simple, pores wide, inconspicuous; reticulate, lumina variable, rounded, muri thick, simplicolumellate, columellae 2.5 µm long, rounded; tectate, wall 3.5 µm thick; 33 µm. Affinity: Dicotyledonae.

Retitricolporites "*colpimarginatus*" (Figs. 322, 323). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore lalongate, annulate; reticulate, lumina < 1 µm wide, muri thin, simplibaculate; tectate, wall 1.8 µm thick; 13 µm. Affinity: Dicotyledonae.

Retitricolporites "*communis*." Ref: figs. 44, 45 (Graham, 1988a). Affinity: Dicotyledonae, Connaraceae, *Rourea* Aubl.

Retitricolporites "*crassiannulatus*" (Figs. 324, 325). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, pore circular, 3.5 µm wide, annulate, annulus 1 µm thick; reticulate, lumina < 1 µm wide, muri sexine strongly columellate, columellae baculae-shaped; tectate, wall 2.5 µm thick; 20 µm. Affinity: Dicotyledonae, Rubiaceae, *Genipa americana* L.

Retitricolporites "*hlongorate*" (Figs. 326, 327). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, 2/3 length of grain, having thick margo broken at equator, pore circular, 2 µm wide, apertures surrounded by a psilate area resembling the "H" condition; reticulate, lumina < 1 µm wide, muri thin, strongly columellate, columellae baculae-shaped; tectate, wall 1.5 µm thick; 18 µm. Affinity: Dicotyledonae.

Retitricolporites "*minibrochatus*" (Figs. 328, 329). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, thin, pore probably elongated, apertures slightly aspidate; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate; tectate, wall 2 µm thick; 22 µm. Affinity: Dicotyledonae.

Retitricolporites "*papilioniformis*" (Figs. 330, 331). Suboblate to oblate-spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, straight, pores lalongate, 4 × 7 µm; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae conspicuous; tectate, wall 2.5 µm thick; 16.5 × 18 µm. Affinity: Dicotyledonae, Fabaceae-Faboideae, *Machaerium* Pers.

Retitricolporites "*pluricolumellatus*." Ref: figs. 99, 100 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 7.

Retitricolporites "*poricostatus*" (Figs. 332, 333). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores annulate, ellip-

soidal; reticulate, lumina uniform, 1 µm wide, muri thin; tectate, wall 1 µm thick; 25 × 21 µm. Affinity: Dicotyledonae.

Retitricolporites "*spheroidalis*" (Figs. 334, 335). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending half the length of the grain, thin, acute ends, marginate, margo displaying costae digitatus, pore slightly elongated; reticulate, lumina < 1 µm wide, muri thin, simplicolumellate; tectate, wall 1.5–2 µm thick; 18 µm. Affinity: Dicotyledonae.

Retitricolporites "*triangularis*" (Figs. 336, 337). Spherical, amb triangular; tricolporate, colpus equatorially arranged, equidistant, extending 2/3 length of grain, thin, acute ends, pores inconspicuous; reticulate, lumina < 1 µm wide, muri thin; tectate, wall 1 µm thick; 16.5 µm. Affinity: Dicotyledonae.

Retitricolporites "*zonoaperturatus*" (Figs. 338, 339). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, marginate, margo thick, pori elongated, joining at apices, resembling an equatorial endocingulum condition; reticulate, lumina < 1 µm wide; tectate; 26 × 23 µm. Affinity: Dicotyledonae.

Retitricolporites CU456. Ref: figs. 54, 55 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Cupania* L.

Retitricolporites CU456-2. Ref: fig. 80 (Graham, 1988a). Affinity: Dicotyledonae, Malvaceae–Byttneroideae, *Guazuma* Mill.

Retitricolporites CU57. Ref: fig. 81 (Graham, 1988a). Affinity: Dicotyledonae, Unknown Type 1.

PLATE 10. Figures 311–358.

311, 312. *Retistephanoporites* aff. *crassiannulatus* SL G27-1, EF O-48/2, Gatun Fm. –8.9 Ma.
313. *Retitrescolpites* "amanoensis" SL 193, EF F-11/4, Cayo Agua Fm. –4.25 Ma.
314, 315. *Retitrescolpites* "usualis" SL G26-1, EF H-8/2, Gatun Fm. –10.0 Ma.
316, 317. *Retitricolpites* "generalis" SL 176, EF H-14/2=4, Tuira Fm. –6.95 Ma.
318, 319. *Retitricolpites* "pseudosimplex" SL La Boca 37.5, EF P-54, Culebra Fm. –19.33 Ma.
320, 321. *Retitricolporites* "amplibrochatus" SL 38, EF H-7/2=4, Tuira Fm. –10.15 Ma.
322, 323. *Retitricolporites* "colpimarginatus" SL G27-2, EF L-39/4, Tuira Fm. –6.95 Ma.
324, 325. *Retitricolporites* "crassiannulatus" SL 175, EF L-13/2, Tuira Fm. –10.15 Ma.
326, 327. *Retitricolporites* "hlongorate" SL 63, EFV-15/2=4, Cayo Agua Fm. –4.25 Ma.
328, 329. *Retitricolporites* "minibrochatus" SL 5a, EF H-14/2, Gatun Fm. –5.6 Ma.
330, 331. *Retitricolporites* "papilioniformis" SL 18, EF Q-7/2=4, Tuira Fm. –10.15 Ma.
332, 333. *Retitricolporites* "poricostatus" SL 1617, EF Q-12/4, Chucunaque Fm. –6.95 Ma.
334, 335. *Retitricolporites* "spheroidalis" SL 19, EF R-38/1, Gatun Fm. –5.6 Ma.
336, 337. *Retitricolporites* "triangularis" SL 391, EF M-51/2, Nancy Point Fm. –5.65 Ma.
338, 339. *Retitricolporites* "zonoaperturatus" SL 1612, EF K-8, Pucro Fm. –6.95 Ma.
340, 341. *Retitriporites* "erythrinoides" SL 391, EF T-43, Tuira Fm. –12.6 Ma.
342, 343. *Retitriporites* "heterobrochatus" SL 184, EF F-22/3, Shark Hole Point Fm. –2.05 Ma.
344, 345. *Retitriporites* "vestibulatum" SL G26-1, EF S-19/1, Gatun Fm. –9.6 Ma.
346. *Rhoipites* "colpizonatus" SL La Boca 37.5, EF O-55/2, Culebra Fm. –19.46 Ma.
347. *Rousea* "cristatus" SL Culebra 15.25, EF Q-29/4, Culebra Fm. –19.12 Ma.
348, 349. *Scabraperiporites* "nothofaguiformis" SL 62, EF G-22/3, Gatun Fm. –5.6 Ma.
350, 351. *Scabrastephanoporites* "apocynaceous" SL 175, EF Q-8/4, Escudo Veraguas Fm. –2.05 Ma.
352. *Siltaria* "comunis" SL Culebra 6.75, EF O-40/2, Culebra Fm. –19.16 Ma.
353. *Stephanoporites* "scabratus" SL 2202, EF O-10/2, Shark Hole Point Fm. –4.6 Ma.
354. *Striatopollis catatumbus* SL 17, EF F-19/1, Gatun Fm. –11.55 Ma.
355, 356. *Striatricolporites* "burseriformis" SL G26-1, EF E-14/2, Tuira Fm. –6.95 Ma.
357, 358. *Striatricolporites melenae* SL 176, EF L-24/2, Cayo Agua Fm. –4.25 Ma.

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Retitriporites "*erythrinoides*" (Figs. 340, 341). Suboblate, amb circular; triporate, pores equatorially arranged, equidistant, circular, 5–6 µm wide; reticulate, lumina rounded, variable, decreasing toward apertures, becoming micropitted, resembling rugulate condition; tectate, wall 1.5 µm thick; 21 µm. Affinity: Dicotyledonae, Fabaceae-Faboideae, *Erythrina* L.

Retitriporites "*heterobrochatus*" (Figs. 342, 343). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, 3 µm wide; reticulate, lumina variable, muri 1 µm thick, simplicolumellate, columellae baculae-shaped; tectate, wall 3.5 µm thick; 32 µm. Affinity: Dicotyledonae.

Retitriporites "*vestibulatum*" (Figs. 344, 345). Suboblate, amb circular; triporate, pores equatorially arranged, equidistant, lolongate, 3 × 2 µm, acute ends, margins irregular; reticulate, lumina <1 µm wide; tectate, wall 1.8 µm thick, muri simplicolumellate, columellae clavate-shaped; 19 × 24 µm. Affinity: Dicotyledonae, Rubiaceae.

Rhoipites aff. *cienagensis*. Ref: ID 793 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Rhoipites "*colpizonatus*" (Fig. 346). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, ca. 22 µm long, simple, margins straight, ends pointed, pores lalongate; reticulate, lumina 1µm wide; tectate, wall 1.5 µm thick; 24.7 µm. Affinity: Dicotyledonae.

Rhoipites guianensis. Ref: ID 794 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sterculiaceae, *Firmiana* Marsili, *Hildegardia* Schott & Endl., *Glossostemon* Desf., *Pterocymbium* R. Br., *Sterculia* L.

Rousea "*cristatus*" (Fig. 347). Prolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, margins straight, ends pointed, 3.5 µm wide; reticulate to micropitted, lumina 1 µm wide, angular, densely distributed; semitectate, wall thin; 29 µm. Affinity: Dicotyledonae.

Rubiaceae (*Cosmibuena*). Ref: fig. 43 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Cosmibuena* Ruiz & Pav.

Rubiaceae (*Posoqueria*). Ref: figs. 51–53 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Posoqueria* Aubl.

Rubiaceae (Type 1). Ref: fig. 41 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Faramea* Type 1.

Rubiaceae (Type 2). Ref: figs. 44, 45, 48 (Graham, 1991b). Affinity: Dicotyledonae, Rubiaceae, *Faramea* Type 2.

Rutaceae (*Casimiroa*). Ref: figs. 46, 47, 49 (Graham, 1991b). Affinity: Dicotyledonae, Rutaceae, *Casimiroa* La Llave & Lex.

Sapindaceae (*Paullinia*). Ref: fig. 50 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Paullinia* L.

Sapindaceae (*Serjania*). Ref: fig. 56 (Graham, 1991b). Affinity: Dicotyledonae, Sapindaceae, *Serjania* Mill.

Sapotaceae (cf. *Bumelia*). Ref: fig. 58 (Graham, 1991b). Affinity: Dicotyledonae, Sapotaceae, cf. *Bumelia* Sw.

Scabraperiporites "*nothofaguiformis*" (Figs. 348, 349). Spherical, amb circular; periporate, pores 6 to 7, circular, ca. 3 µm wide, slightly annulate, not well defined, appearing as pseudopori; scabrate; tectate, wall 1 µm thick; 21 µm. Affinity: Dicotyledonae, Fagaceae, *Nothofagus dombeyi* (Mirb.) Oerst.

Scabrastephanoporites "*apocynaceous*" (Figs. 350, 351). Spherical, amb circular; stephanoporate, pores equatorially arranged, circular, ca. 1.5 µm wide, annulate, annulus < 1 µm wide; scabrate; tectate, wall 1 µm thick; 18 µm. Affinity: Dicotyledonae, Apocynaceae.

Siltaria "*comunis*" (Fig. 352). Spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, margins straight, ends pointed, pores circular, costate; micropitted; tectate, wall 1 µm thick; 19 µm. Affinity: Dicotyledonae.

Siltaria dilcheri. Ref: ID 2075 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Stephanoporites "*scabratus*" (Fig. 353). Suboblate, amb circular; stephanoporate, pores 5, circular, vestibulate; reticulate, lumina < 1 µm wide, muri thin; tectate, wall 2.5–3 µm thick; 17 × 22 µm. Affinity: Dicotyledonae.

Striatopollis catatumbus (Fig. 354). Subprolate, amb probably circular; tricolpate, colpus equatorially arranged, equidistant, extending 3/4 length of grain, wide, costate, irregular; striate, striae dense, longitudinally oriented, 1 µm wide; tectate, wall 1.5 µm thick; 32 × 22 µm. Ref: ID 2075 (Jaramillo & Rueda, 2013); fig. 31 (Graham, 1988b); figs. 37, 38 (Graham, 1989); fig. 25 (Graham, 1991b). Affinity: Dicotyledonae, Fabaceae, *Crudia* Schreb., *Anthonotha* P. Beauv., *Isoberlinia* Craib & Stapf ex Holland, *Macrolobium bifolium* (Aubl.) Pers.

Striatricolporites "*burseriformis*" (Figs. 355, 356). Oblate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pori lalongate, 1 × 4 µm, slightly protruding, costate, annulus inconspicuous; reticulate-striate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae baculae-shaped, striae longitudinally oriented; tectate, wall 1.8 µm thick; 15 × 16.5 µm. Ref: fig. 12 (Graham, 1991b). Affinity: Dicotyledonae, Burseraceae, *Bursera simaruba* (L.) Sarg.

Striatricolporites digitatus. Ref: ID 883 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Striatricolporites melenae (Figs. 357, 358). Prolate, amb probably circular; tricolporate, colpus equatorially arranged, equidistant, extending 2/3 length of grain, thin, pori circular, 2 µm wide, slightly protruding, costate, annulus inconspicuous; reticulate-striate, lumina < 1 µm wide, muri thin, simplicolumellate, columellae baculae-shaped, striae longitudinally oriented; tectate, wall 1.8 µm thick; 22 × 14 µm. Ref: ID 883 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Anacardiaceae?

Striatricolporites tenuissimus. Ref: ID 888 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Symplocaceae (*Symplocos*). Ref: fig. 59 (Graham, 1991b). Affinity: Dicotyledonae, Symplocaceae, *Symplocos* Jacq. Type 1.

Syncolporites "*paraisus*." Ref: ID 2095 (Jaramillo & Rueda, 2013); fig. 77 (Graham, 1988a). Affinity: Dicotyledonae, Sapindaceae, *Matayba* Aubl.

Syncolporites poricostatus. Ref: ID 900 (Jaramillo & Rueda, 2013); figs. 65, 66 (Graham, 1988a); fig. 32 (Graham, 1988b); fig. 28 (Graham, 1991b). Affinity: Dicotyledonae, Myrtaceae, *Eugenia* L./*Myrcia* DC. types.

Tetracolpites "*rectangularis*" (Figs. 359, 360). Oblate, amb rectangular; stephanocolpate, colpi 4, colpus equatorially arranged, equidistant, extending nearly entire length of grain, wide, irregular; perforate; tectate, wall 1.5 µm thick; 22 µm. Affinity: Dicotyledonae.

Tetracolporites "*guareaensis*" (Figs. 361–363). Oblate, amb rectangular; stephanocolpate, colpori 4,

colpus equatorially arranged, equidistant, short, very thin, pore slightly oval, having subtle costae, annulus thin; psilate; tectate, wall 1 µm thick; 18 µm. Ref: figs. 39, 42 (Graham, 1991b). Affinity: Dicotyledonae, Meliaceae, *Guarea* F. Allam. ex L.

Tetracolporites "*trichiliensis*" (Figs. 364–366). Subprolate, amb circular; stephanocolporate, colpori 4, colpus equatorially arranged, equidistant, colpus 2/3 length of grain, thin, pores lalongate-ellipsoidal, 2 × 8 µm, costate, costae ca. 2 µm thick; reticulate, lumina < 1 µm wide, muri simplicolumellate; tectate, wall 1 µm thick at intercolpium area and 2.5 µm at apertural area; 20 × 16.5 µm. Affinity: Dicotyledonae, Meliaceae, *Trichilia* P. Browne.

Tetracolporites "*vestibulatum*" (Figs. 367, 368). Spherical, amb circular; stephanocolporate, colpori 4, colpus equatorially arranged, equidistant, short, 4–5 µm long, pores circular, 2.5–3 µm wide, annulate, vestibulate; psilate, slightly scabrate; tectate, wall 1.5 µm thick; 26 µm. Affinity: Dicotyledoneae.

Tetracolporopollenites maculosus. Ref: ID 909 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapotaceae, *Chrysophyllum argenteum* Jacq.

Tetracolporopollenites aff. *spongiosus*. Ref: ID 912 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae.

Tetracolporopollenites transversalis. Ref: ID 913 (Jaramillo & Rueda, 2013). Affinity: Dicotyledonae, Sapotaceae, subtype VII-A of Harley (1991), *Micropholis* (Griseb.) Pierre.

Tiliaceae (*Mortoniodendron*). Ref: fig. 61 (Graham, 1991b). Affinity: Dicotyledonae, Tiliaceae, *Mortoniodendron* Standl. & Steyerm.

Tricolpites "*minutibacularis*" (Figs. 369–371). Subprolate, amb circular; tricolpate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, marginate, margo surrounded by small baculae; baculate; intectate, wall 1.2 µm thick; 20 × 17 µm. Affinity: Dicotyledonae.

Tricolpites "*punctatus*." Ref: figs. 87–90 (Graham, 1988b). Affinity: Dicotyledonae, Unknown Type 3.

Tricolporites "*annulatus*" (Figs. 372–374). Spherical, amb triangular to circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, pore annulate; retic-

PLATE 11. Figures 359–399.
359, 360. *Tetracolpites* "rectangularis" SL 1553, EF P-5/4, Tuira Fm. –6.95 Ma.
361–363. *Tetracolporites* "guareaensis" SL 5b, EF N-12/2=4, Gatun Fm. –5.6 Ma.
364–366. *Tetracolporites* "trichiliensis" SL G27-2, EF T-6/1, Tuira Fm. –10.15 Ma.
367, 368. *Tetracolporites* "vestibulatum" SL 11, EF C-18/4=D-18/2, Gatun Fm. –5.6 Ma.
369–371. *Tricolpites* "minutibacularis" SL 68, EF K-22, unnamed Fm. –3.55 Ma.
372–374. *Tricolporites* "annulatus" SL 2179, EF E-48, Cayo Agua Fm. –4.25 Ma.
375–378. *Tricolporites* "colpidigitatus" SL G26-1, EF V-6, Gatun Fm. –9.6 Ma.
379–381. *Tricolporites* "ericipitiformis" SL G28-1, EF H-45/4, Tuira Fm. –6.95 Ma.
382, 383. *Tricolporites* "megaporatus" SL 177, EF O-26/3, Cayo Agua Fm. –4.25 Ma.
384, 385. *Venezuelites* "centroamericanus" SL La Boca 8.5, EF X-38/2, Culebra Fm. –19.49 Ma.
386, 387. *Verrutricolporites* "desmodiensis" SL 65, EF L-21/1, Cayo Agua Fm. –4.25 Ma.
388, 389. *Verrutricolporites* "faboides" SL 169, EF H-46/1, Tuira Fm. –6.95 Ma.
390, 391. *Verrutricolporites* "poricircularis" SL 1553, EF D-13/2, Tuira Fm. –6.95 Ma.
392–394. *Vochysia* Type SL 174, EF E-21/4, Gatun Fm. –11.55 Ma.
395, 396. *Zonocostites* "elongatus" SL Culebra 1.5, EFS-43, Culebra Fm. –19.18 Ma.
397–399. *Zonocostites ramonae* SL 174, EF D-19/3, Tuira Fm. –12.6 Ma.

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ulate, lumina < 1 µm wide, appearing almost psilate; tectate, wall variable, 1 µm thick at apertural area, cavate at intercolpium area, cavea 1 µm long; 24 µm. Affinity: Dicotyledonae.

Tricolporites "*colpidigitatus*" (Figs. 375–378). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, thin, 1 µm wide, marginate, margo bifurcated at equator (exitus digitus), pore elongated, not well defined; apparently clavate, resembling reticulate pattern; tectate, wall 2–2.5 µm thick, sexine 1.5 µm thick, strongly columellate, columellae baculae-like, thin, nexine < 1 µm thick; 20 × 19 µm. Affinity: Dicotyledonae.

Tricolporites "*ericipitiformis*" (Figs. 379–381). Suboblate, amb circular-triangular; tricolporate, colpus equatorially arranged, equidistant, 22 × 2.5 µm, marginate, margo 2.5 µm thick, almost joining at polar area, pores elongated, surrounded by a psilate area resembling the "H" condition; psilate; tectate, wall 2 µm thick; 19 × 22 µm. Affinity: Dicotyledonae, Ericaceae.

Tricolporites "*megaporatus*" (Figs. 382, 383). Spherical, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, subtle, wide, acute ends, pores circular, 5 µm wide, annulate, annulus 2.5 µm thick; baculate, baculae < 1 µm long, dense; intectate, wall 1 µm thick; 32 µm. Affinity: Dicotyledonae.

Unknown 1. Ref: figs. 65, 66 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 1.

Unknown 2. Ref: figs. 67, 68 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 2.

Unknown 4. Ref: fig. 71 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 4.

Unknown 6. Ref: fig. 73 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 6.

Unknown 7. Ref: figs. 74–77 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 7.

Unknown 8. Ref: fig. 78 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 8.

Unknown 9. Ref: figs. 79, 80 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 9.

Unknown 10. Ref: fig. 81 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 10.

Unknown 11. Ref: fig. 82 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 11.

Unknown 12. Ref: fig. 83 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 12.

Unknown 13. Ref: fig. 84 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 13.

Unknown 14. Ref: fig. 85 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 14.

Unknown 15. Ref: fig. 86 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 15.

Unknown 16. Ref: fig. 92 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 16.

Unknown 17. Ref: fig. 91 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 17.

Unknown 18. Ref: figs. 87, 88 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 18.

Unknown 19. Ref: figs. 97, 98 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 19.

Unknown 20. Ref: figs. 89, 90 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 20.

Unknown 21. Ref: fig. 95 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 21.

Unknown 22. Ref: fig. 94 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 22.

Unknown 23. Ref: fig. 96 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 23.

Unknown 24. Ref: fig. 93 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 24.

Unknown 25. Ref: figs. 100, 101 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 25.

Unknown 26. Ref: figs. 102, 103 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 26.

Unknown 27. Ref: fig. 99 (Graham, 1991b). Affinity: Dicotyledonae, Unknown Type 27.

Utricularia. Ref: ID 950 (Jaramillo & Rueda, 2013); fig. 30 (Graham, 1991b); fig. 36 (Graham, 1989). Affinity: Dicotyledonae, Lentibulariaceae, *Utricularia* L.

Venezuelites "*centroamericanus*" (Figs. 384, 385). Oblate, amb circular; stephanoporate, pores 4, circular, 1 µm wide, costate, annulus thick; psilate; wall 3 µm thick; 25 µm. Affinity: Dicotyledonae.

Verbenaceae (*Aegiphila*). Ref: figs. 62, 63 (Graham, 1991b). Affinity: Dicotyledonae, Verbenaceae, *Aegiphila* Jacq.

Verbenaceae (*Petrea*). Ref: fig. 64 (Graham, 1991b). Affinity: Dicotyledonae, Verbenaceae, *Petrea* L.

Verrutricolporites "*desmodiensis*" (Figs. 386, 387). Suboblate, amb circular, slightly angular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, pores inconspicuous, masked by ornamentation; verrucate, verrucae flat, wide, 2 µm long; tectate, wall 6 µm thick; 48 µm. Affinity: Dicotyledonae, Fabaceae–Faboideae, *Desmodium* Desv.

Verrutricolporites "*faboides*" (Figs. 388, 389). Oblate, amb circular; tricolporate, colpus equatorially arranged, equidistant, short, 12 × 1 µm, surrounded by dense patches of verrucae resembling a thick margo, pore lineal-elongated, 1 × 8 µm; verrucate, verrucae variable in shape and size; tectate, wall > 3 µm thick, masked by sculpture; 18 × 31 µm. Affinity: Dicotyledonae, Fabaceae-Faboideae.

Verrutricolporites "*poricircularis*" (Figs. 390, 391). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, 3/4 length of grain, inconspicuous, pores circular, 2 µm wide; verrucate, verrucae flat, variable in size; tectate, wall 1–1.5 µm thick; 18 × 17 µm. Affinity: Dicotyledonae.

Vochysia Type (Figs. 392–394). Suboblate, amb circular-hexagonal, concave; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain × 1.5 µm wide, rounded ends, pores elongated, surrounded by a psilate area resembling the "H" condition; psilate; tectate, wall > 3 µm thick, masked by sculpture, densely columellate; 18–19 µm. Affinity: Dicotyledonae,Vochysiaceae, *Vochysia* Aubl.

Zonocostites "*elongatus*" (Figs. 395, 396). Subprolate, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, simple, pores apparently lalongate, inconspicuous; psilate to micropitted; tectate, wall 1 µm thick; 26.5 × 22 µm. Affinity: Dicotyledonae.

Zonocostites ramonae (Figs. 397–399). Prolate spheroidal, amb circular; tricolporate, colpus equatorially arranged, equidistant, extending nearly entire length of grain, thin, pores lalongate, joining at apices, displaying a continuous equatorial ring, costate, costae slightly protruding; psilate; tectate, wall 1.8 µm thick; 12 × 11 µm. Ref: ID 975 (Jaramillo & Rueda, 2013); figs. 67–70 (Graham,

1988a); figs. 33, 34 (Graham, 1988b); fig. 47 (Graham, 1989), fig. 29 (Graham, 1991b). Affinity: Dicotyledonae, Rhizophoraceae, *Rhizophora* L., *Bruguiera* Lam., *Ceriops* Arn., *Carallia* Roxb. types.

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APPENDIX 3. Code for the analysis used in this paper using the R Project for Statistical Computing syntaxis (R Development Core Team, 2012).

```
library(permute)
library(vegan)
count.temp<-read.delim("count_data.txt", header = FALSE, sep = "\t",na.strings = "NA")#count data
count.temp=as.matrix(count.temp)
age=count.temp[1,]
count.graham=count.temp[2:nrow(count.temp),]
count.graham[is.na(count.graham)] = 0

origin<-read.delim("origin.txt", header = TRUE, sep = "\t",na.strings = "NA")#family origin
locality=read.delim("sample_area.txt", header = TRUE, sep = "\t",na.strings = "NA")# samples site

BCI.temp<-read.delim("BCI.txt", header = TRUE, sep = "\t",na.strings = "NA")#BCI data
BCI.count=as.matrix(BCI.temp[,1:2])
BCI.per=prop.table(BCI.count, 2)#BCI table in percentages


##abundances in absolute counts
totalcount=apply(count.graham,2, sum)#counts per sample
angiosperms=apply(count.graham[which(origin[,3]=="Angiosperm"),],2, sum)##sum angiosperms
```

```
gymnosperms=count.graham[which(origin[,3]=="Gymnosperm"),]#only one gymnosperm
ferns=apply(count.graham[which(origin[,3]=="Spore"),],2, sum)#
marine=apply(count.graham[which(origin[,3]=="Marine"),],2, sum)#


#abundances in percentages
perc.graham=prop.table(count.graham, 2)#table in percentages

age.80=age[which(totalcount>80)]##ages for samples >80

##ONLY SAMPLES WITH COUNTS LARGER THAN 80 grains
angiosperms.per=apply(perc.graham[which(origin[,3]=="Angiosperm"),which(totalcount>80)],2,
sum)##sum angiosperms
gymnosperms.per=perc.graham[which(origin[,3]=="Gymnosperm"),which(totalcount>80)]#only one
gymnosperm
ferns.per=apply(perc.graham[which(origin[,3]=="Spore"),which(totalcount>80)],2, sum)#
marine.per=apply(perc.graham[which(origin[,3]=="Marine"),which(totalcount>80)],2, sum)#

par(mfrow = c(1, 4))##FIGURE ANGIOSPERMS OVER TIME
plot(angiosperms.per,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1),xlab="Proportion of indi-
viduals", ylab="age(My)", main="angiosperms")
abline(h=3.5)#
abline(h=10)#
text(0.9, 2, round(mean(100*angiosperms.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.9, 7, round(mean(100*angiosperms.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.9, 15, round(mean(100*angiosperms.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(gymnosperms.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of in-
dividuals", ylab="age(My)",main="gymnosperms")
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*gymnosperms.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*gymnosperms.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*gymnosperms.per[which(age.80>10)],na.rm = TRUE),3),cex = .75)
plot(ferns.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of individuals",
ylab="age(My)",main="ferns and allies")
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*ferns.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*ferns.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 15, round(mean(100*ferns.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(marine.per,age[which(totalcount>80)], xlim=c(0,1),ylim=c(20,0),xlab="Proportion of individu-
als", ylab="age(My)", main="marine")
```

```
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*marine.per[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*marine.per[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.8, 15, round(mean(100*marine.per[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE

t.test(angiosperms.per[which(age.80>10)],angiosperms.per[which(age.80<10 & age.80>3.5)])#>10
0.40, 10-3.5 0.36, p 0.2, df 109; angiosperms proportion do not differ from the 3.5 to 19.5 My
interval
t.test(angiosperms.per[which(age.80<10 & age.80>3.5)],angiosperms.per[which(age.80<3.5)])#10-3.5
0.36, <3.5 0.26, p 0.07, df 17.

t.test(ferns.per[which(age.80>10)],ferns.per[which(age.80<10 & age.80>3.5)])#>10 0.59, 10-3.5 0.62,
p 0.3, DF 108 ferns proportion do not differ from the 3.5 to 19.5 My interval
t.test(ferns.per[which(age.80<10 & age.80>3.5)],ferns.per[which(age.80<3.5)])#10-3.5 0.62, >10
0.73, p 0.009, dF 17


#INDIVIDUAL ANALYSIS abundances in percentages per origin, counts larger than 80 grains
Amazonian.or=apply(perc.graham[which(origin[,2]=="Gondwana-Amazonian centered"),which(total-
count>80)],2, sum)##sum angiosperms
Andean.or=apply(perc.graham[which(origin[,2]=="Gondwana-Northern Andean centered"),which
(totalcount>80)],2, sum)#only one gymnosperm
Southern.or=apply(perc.graham[which(origin[,2]=="Gondwana-Southern Andean centered"),which
(totalcount>80)],2, sum)#
Laurasia.or=apply(perc.graham[which(origin[,2]=="Laurasia"),which(totalcount>80)],2, sum)#


BCI.Az=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Amazonian centered"),1])##data %indiv
for BCI
BCI.Andes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Northern Andean centered"),1])
BCI.SouthAndes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Southern Andean centered"),1])
BCI.Laur=sum(BCI.per[which(BCI.temp[,3]=="Laurasia"),1])
BCI.Unk=sum(BCI.per[which(BCI.temp[,3]=="Unassigned"),1])

unknown.or=1-(Amazonian.or+Andean.or+Southern.or+Laurasia.or)#percentage of unknown abun-
dance of species per sample
plot(unknown.or,age[which(totalcount>80)], ylim=c(20,0),xlab="Proportion of individuals", ylab=
"age(My)", main="Proportion of individuals with unknown natural affinities")##FIGURE unknown
SP
length(which(is.na(origin$Origin)==FALSE))##how many unknown taxa
```

```
par(mfrow = c(1, 5))##FIGURE ORIGIN OVER TIME, % of individuals in assemblage
plot(Amazonian.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="Gondwana\nAmazonian centered",cex.main=1)
points(BCI.Az,0)
text(0.8, 0, round(mean(100*BCI.Az),1),cex = .75)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*Amazonian.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Amazonian.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Amazonian.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Andean.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of individuals", ylab="age(My)",main="Gondwana\nNorthern Andean centered",cex.main=1)
points(BCI.Andes,0)
text(0.8, 0, round(mean(100*BCI.Andes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Andean.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Andean.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Andean.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Southern.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of individuals", ylab="age(My)",main="Gondwana\nSouthern Andean centered",cex.main=1)
points(BCI.SouthAndes,0)
text(0.8, 0, round(mean(100*BCI.SouthAndes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Southern.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Southern.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Southern.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Laurasia.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of individuals", ylab="age(My)", main="Laurasia",cex.main=1)
points(BCI.Laur,0)
text(0.8, 0, round(mean(100*BCI.Laur),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Laurasia.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Laurasia.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Laurasia.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(unknown.or,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of individuals", ylab="age(My)", main="Unknown",cex.main=1)
points(BCI.Unk,0)
```

```
text(0.8, 0, round(mean(100*BCI.Unk),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*unknown.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*unknown.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.1, 15, round(mean(100*unknown.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END OF FIGURE

t.test(Amazonian.or[which(age.80>3.5)],Amazonian.or[which(age.80<3.5)])#
t.test(Laurasia.or[which(age.80>3.5)],Laurasia.or[which(age.80<3.5)])#
t.test(Andean.or[which(age.80>3.5)],Andean.or[which(age.80<3.5)])#
t.test(Amazonian.or[which(age.80<10 & age.80>3.5)],Amazonian.or[which(age.80>10)])#
t.test(Laurasia.or[which(age.80<10 & age.80>3.5)],Laurasia.or[which(age.80>10)])#

summary (Amazonian.or)##summary data Amazonian centered, # of individuals
summary (Andean.or)
summary (Southern.or)
summary (Laurasia.or)
summary(unknown.or)
sd(unknown.or)

##SPECIES ANALYSIS
pa.graham=perc.graham##presence absence table
pa.graham[(pa.graham>0)]=1## only presence/absence
paper.graham=prop.table(pa.graham, 2)#presence/absence in percentages

Amazonian.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Amazonian centered"),which
(totalcount>80)],2, sum)##sum angiosperms
Andean.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Northern Andean centered"),which
(totalcount>80)],2, sum)#only one gymnosperm
Southern.sp=apply(paper.graham[which(origin[,2]=="Gondwana-Southern Andean centered"),which
(totalcount>80)],2, sum)#
Laurasia.sp=apply(paper.graham[which(origin[,2]=="Laurasia"),which(totalcount>80)],2, sum)#

BCIsp.Az=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Amazonian centered"),2])##data %sp for
BCI
BCIsp.Andes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Northern Andean centered"),2])
BCIsp.SouthAndes=sum(BCI.per[which(BCI.temp[,3]=="Gondwana-Southern Andean centered"),2])
BCIsp.Laur=sum(BCI.per[which(BCI.temp[,3]=="Laurasia"),2])
BCIsp.Unk=sum(BCI.per[which(BCI.temp[,3]=="Unassigned"),2])

unknown.sp=1-(Amazonian.sp+Andean.sp+Southern.sp+Laurasia.sp)#percentage of unknown species
per sample
```

```
plot(unknown.sp,age[which(totalcount>80)], ylim=c(20,0),xlab="Proportion of species", ylab="age(My)", main="Proportion of species with unknown origin")##


par(mfrow = c(1, 5))##FIGURE ORIGIN OVER TIME, % of species in assemblage
plot(Amazonian.sp,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of species", ylab="age(My)", main="Gondwana\nAmazonian centered",cex.main=1)
points(BCIsp.Az,0)
text(0.8, 0, round(mean(100*BCIsp.Az),1),cex = .75)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*Amazonian.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Amazonian.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Amazonian.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Andean.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)",main="Gondwana\nNorthern Andean centered",cex.main=1)
points(BCIsp.Andes,0)
text(0.8, 0, round(mean(100*BCIsp.Andes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Andean.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Andean.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Andean.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Southern.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)",main="Gondwana\nSouthern Andean centered",cex.main=1)
points(BCIsp.SouthAndes,0)
text(0.8, 0, round(mean(100*BCIsp.SouthAndes),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Southern.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Southern.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
text(0.8, 15, round(mean(100*Southern.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(Laurasia.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species", ylab="age(My)", main="Laurasia",cex.main=1)
points(BCIsp.Laur,0)
text(0.8, 0, round(mean(100*BCIsp.Laur),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.8, 2, round(mean(100*Laurasia.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*Laurasia.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1), cex = .75)
```

```
text(0.8, 15, round(mean(100*Laurasia.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(unknown.sp,age[which(totalcount>80)], ylim=c(20,0),xlim=c(0,1),xlab="Proportion of species",
ylab="age(My)", main="Unknown",cex.main=1)
points(BCIsp.Unk,0)
text(0.8, 0, round(mean(100*BCIsp.Unk),1),cex = .75)
abline(h=3.5)#
abline(h=10)
text(0.1, 2, round(mean(100*unknown.sp[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*unknown.sp[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),
cex = .75)
text(0.1, 15, round(mean(100*unknown.sp[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END OF FIGURE

t.test(Amazonian.sp[which(age.80>3.5)],Amazonian.sp[which(age.80<3.5)])#
t.test(Laurasia.sp[which(age.80>3.5)],Laurasia.sp[which(age.80<3.5)])#
t.test(Andean.sp[which(age.80>3.5)],Andean.sp[which(age.80<3.5)])#
t.test(Amazonian.sp[which(age.80<10 & age.80>3.5)],Amazonian.sp[which(age.80>10)])#
t.test(Laurasia.sp[which(age.80<10 & age.80>3.5)],Laurasia.sp[which(age.80>10)])#

mean (Amazonian.sp)##summary data Amazonian centered, # of species
sd (Amazonian.sp)
mean (Andean.sp)
sd (Andean.sp)
mean (Southern.sp)
sd (Southern.sp)
mean (Laurasia.sp)
sd (Laurasia.sp)
mean(unknown.sp)
sd(unknown.sp)

##ECOLOGICAL ANALYSES
ecol<-read.delim("ecology.txt", header = TRUE, sep = "\t",na.strings = "NA")#count data
ecol[is.na(ecol)] = 0
Uk.temp=apply(ecol,1, sum)#species that do have any ecology

#proportion individuals
TRFO.or=apply(perc.graham[which(ecol$TRFO==1),which(totalcount>80)],2, sum)##sum TRFO
PMF.or=apply(perc.graham[which(ecol$PMF==1),which(totalcount>80)],2, sum)##sum
MF.or=apply(perc.graham[which(ecol$MF==1),which(totalcount>80)],2, sum)##sum
TDFO.or=apply(perc.graham[which(ecol$TDFO==1),which(totalcount>80)],2, sum)##sum
SV.or=apply(perc.graham[which(ecol$SV==1),which(totalcount>80)],2, sum)##sum
FW.or=apply(perc.graham[which(ecol$FW==1),which(totalcount>80)],2, sum)##sum
MG.or=apply(perc.graham[which(ecol$MG==1),which(totalcount>80)],2, sum)##sum
MR.or=apply(perc.graham[which(ecol$MR==1),which(totalcount>80)],2, sum)##sum
```

```
UK.or=apply(perc.graham[which(Uk.temp==0),which(totalcount>80)],2, sum)##sum

par(mfrow = c(1, 4))##Ecology ORIGIN OVER TIME PART A, % of individuals in assemblage
plot(TRFO.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="PMF")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*PMF.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MF.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="MF")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MF.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TDFO")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE

par(mfrow = c(1, 5))##Ecology ORIGIN OVER TIME PART B, % of individuals in assemblage
plot(SV.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="SV")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*SV.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*SV.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*SV.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
```

```
plot(FW.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals",
ylab="age(My)", main="FW")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*FW.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*FW.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*FW.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MG.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals",
ylab="age(My)", main="MG")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MG.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MG.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MG.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(MR.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals",
ylab="age(My)", main="MR")
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MR.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MR.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*MR.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
plot(UK.or,age[which(totalcount>80)], ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals",
ylab="age(My)", main="UK")
abline(h=3.5)#
abline(h=10)#
text(0.1, 2, round(mean(100*UK.or[which(age.80<3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 7, round(mean(100*UK.or[which(age.80<10 & age.80>3.5)],na.rm = TRUE),1),cex = .75)
text(0.1, 15, round(mean(100*UK.or[which(age.80>10)],na.rm = TRUE),1),cex = .75)
##END FIGURE

round(100*sd(TRFO.or,na.rm = TRUE),2)
round(100*sd(PMF.or,na.rm = TRUE),2)
round(100*sd(MF.or,na.rm = TRUE),2)
round(100*sd(TDFO.or,na.rm = TRUE),2)
round(100*sd(SV.or,na.rm = TRUE),2)
round(100*sd(FW.or,na.rm = TRUE),2)
round(100*sd(MG.or,na.rm = TRUE),2)
round(100*sd(MR.or,na.rm = TRUE),2)
round(100*sd(UK.or,na.rm = TRUE),2)

t.test(MF.or[which(age.80>10)],MF.or[which(age.80<10)])#

famgen<-read.delim("family_genus.txt", header = TRUE, sep = "\t")#family/genus
```

```
length(which(famgen[,1]!="Unknown" & Uk.temp==0)) number of taxa that have a family assignment but not an ecological preference

##SAMPLE AREAS
area<-read.delim("sample_area.txt", header = TRUE, sep = "\t")#family/genus sample_area.txt

#proportion individuals per region
TRFO.pc=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Panama Central")],2, sum)##sum TRFO pc
age.pc=age[totalcount>80 & area[,1]=="Panama Central"]
TRFO.d=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Darien")],2, sum)##sum TRFO d
age.d=age[totalcount>80 & area[,1]=="Darien"]
TRFO.b=apply(perc.graham[which(ecol$TRFO==1), which(totalcount>80 & area[,1]=="Bocas del Toro")],2, sum)##sum TRFO bocas
age.b=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals in assemblage by AREA TRF
plot(TRFO.b,age.b, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nBocas del Toro",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.b[which(age.b<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.b[which(age.b<10 & age.b>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.b[which(age.b>10)],na.rm = TRUE),1),cex = .75)
plot(TRFO.pc,age.pc, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.pc[which(age.pc<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.pc[which(age.pc<10 & age.pc>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.pc[which(age.pc>10)],na.rm = TRUE),1),cex = .75)
plot(TRFO.d,age.d, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)", main="TRFO\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TRFO.d[which(age.d<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TRFO.d[which(age.d<10 & age.d>3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TRFO.d[which(age.d>10)],na.rm = TRUE),1),cex = .75)
##END

PMF.pc=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]=="Panama Central")],2, sum)##sum PMF pc
```

```
age.pcPMF=age[totalcount>80 & area[,1]=="Panama Central"]
PMF.d=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]=="Darien")],2,
sum)##sum PMF darien
age.dPMF=age[totalcount>80 & area[,1]=="Darien"]
PMF.b=apply(perc.graham[which(ecol$PMF==1), which(totalcount>80 & area[,1]=="Bocas del
Toro")],2, sum)##sum PMF bocas
age.bPMF=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals in assemblage by AREA PMF
plot(PMF.b,age.bPMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="PMF\nBocas del Toro",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.b[which(age.bPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.b[which(age.bPMF<10 & age.bPMF>3.5)],na.rm = TRUE),1),cex
= .75)
text(0.8, 15, round(mean(100*PMF.b[which(age.bPMF>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.pc,age.pcPMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="PMF\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.pc[which(age.pcPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.pc[which(age.pcPMF<10 & age.pcPMF>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*PMF.pc[which(age.pcPMF>10)],na.rm = TRUE),1),cex = .75)
plot(PMF.d,age.dPMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="PMF\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*PMF.d[which(age.dPMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*PMF.d[which(age.dPMF<10 & age.dPMF>3.5)],na.rm = TRUE),1),cex
= .75)
text(0.8, 15, round(mean(100*PMF.d[which(age.dPMF>10)],na.rm = TRUE),1),cex = .75)
##END

MF.pc=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]=="Panama Cen-
tral")],2, sum)##sum PMF pc
age.pcMF=age[totalcount>80 & area[,1]=="Panama Central"]
MF.d=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]=="Darien")],2, sum)
##sum PMF darien
age.dMF=age[totalcount>80 & area[,1]=="Darien"]
MF.b=apply(perc.graham[which(ecol$MF==1), which(totalcount>80 & area[,1]=="Bocas del Toro")],
2, sum)##sum PMF bocas
```

```
age.bMF=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals by AREA MF
plot(MF.b,age.bMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="MF\nBocas del Toro",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.b[which(age.bMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.b[which(age.bMF<10 & age.bMF>3.5)],na.rm = TRUE),1),cex =
.75)
text(0.8, 15, round(mean(100*MF.b[which(age.bMF>10)],na.rm = TRUE),1),cex = .75)
plot(MF.pc,age.pcMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="MF\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.pc[which(age.pcMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.pc[which(age.pcMF<10 & age.pcMF>3.5)],na.rm = TRUE),1),cex =
.75)
text(0.8, 15, round(mean(100*MF.pc[which(age.pcMF>10)],na.rm = TRUE),1),cex = .75)
plot(MF.d,age.dMF, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab="age(My)",
main="MF\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*MF.d[which(age.dMF<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*MF.d[which(age.dMF<10 & age.dMF>3.5)],na.rm = TRUE),1),cex =
.75)
text(0.8, 15, round(mean(100*MF.d[which(age.dMF>10)],na.rm = TRUE),1),cex = .75)
##END

TDFO.pc=apply(perc.graham[which(ecol$TDFO==1), which(totalcount>80 & area[,1]=="Panama
Central")],2, sum)##sum PMF pc
age.pcTDFO=age[totalcount>80 & area[,1]=="Panama Central"]
TDFO.d=apply(perc.graham[which(ecol$TDFO==1),which(totalcount>80&area[,1]=="Darien")],2,
sum)##sum PMF darien
age.dTDFO=age[totalcount>80 & area[,1]=="Darien"]
TDFO.b=apply(perc.graham[which(ecol$TDFO==1), which(totalcount>80 & area[,1]=="Bocas del
Toro")],2, sum)##sum PMF bocas
age.bTDFO=age[totalcount>80 & area[,1]=="Bocas del Toro"]

par(mfrow = c(1, 3))##Ecology FIGURE, % of individuals by AREA TDFO
plot(TDFO.b,age.bTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab=
"age(My)", main="TDFO\nBocas del Toro",cex.main=1)
abline(h=3.5)#
```

```
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.b[which(age.bTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.b[which(age.bTDFO<10 & age.bTDFO>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.b[which(age.bTDFO>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.pc,age.pcTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab=
"age(My)", main="TDFO\nPanama Central",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.pc[which(age.pcTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.pc[which(age.pcTDFO<10 & age.pcTDFO>3.5)],na.rm =
TRUE),1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.pc[which(age.pcTDFO>10)],na.rm = TRUE),1),cex = .75)
plot(TDFO.d,age.dTDFO, ylim=c(20,0), xlim=c(0,1), xlab="Proportion of individuals", ylab=
"age(My)", main="TDFO\nDarien",cex.main=1)
abline(h=3.5)#
abline(h=10)#
text(0.8, 2, round(mean(100*TDFO.d[which(age.dTDFO<3.5)],na.rm = TRUE),1),cex = .75)
text(0.8, 7, round(mean(100*TDFO.d[which(age.dTDFO<10 & age.dTDFO>3.5)],na.rm = TRUE),
1),cex = .75)
text(0.8, 15, round(mean(100*TDFO.d[which(age.dTDFO>10)],na.rm = TRUE),1),cex = .75)
##END

t.test(c(MF.pc[which(age.pcMF >3.5 & age.pcMF<10)],MF.b[which(age.bMF >3.5 & age.bMF<10)]),
MF.d[which(age.dMF >3.5 & age.dMF<10)])

##diversity
diversity.35 <- specaccum(t(count.graham[,which(age<3.5 & totalcount>80)]))
diversity.1035 <- specaccum(t(count.graham[,which(age<10 & age>3.5 & totalcount>80)]))
diversity.2010 <- specaccum(t(count.graham[,which(age>10 & totalcount>80)]))

plot(diversity.1035,col="red", lwd=2, ci.lty=0, ci.col="red", xlim=c(0,60), xlab="samples", ylab="num-
ber of species")##FIGURE SPECIES ACCUMULATION CURVE
plot(diversity.35,col="purple", add=TRUE)
plot(diversity.1035,col="red", add=TRUE)
plot(diversity.2010,col="blue", add=TRUE)
legend(0, 350, c("<3.5 Ma","3.5-10 Ma", "10-19.5 Ma"), cex=0.8,
  col=c("purple","red","blue"), lty=1)
  ##END

diverColl.1035 <- specaccum(divetemp[which(divetemp[,1]<10 & divetemp[,1]>3.5),2:ncol(dive-
temp)], method = 'collector')
diverColl.35 <- specaccum(divetemp[which(divetemp[,1]<3.5),2:ncol(divetemp)], method = 'collector')
diverColl.10 <- specaccum(divetemp[which(divetemp[,1]>10),2:ncol(divetemp)], method = 'collector')
```

```
plot(divetemp[which(divetemp[,1]<10 & divetemp[,1]>3.5),1]+6.59204-10.14304,diverColl.1035$
richness, xlab="Time Interval (Ma)",ylab="number of species",xlim=c(0,10), pch=2)##FIGURE A
COLLECTORS CURVE
points(divetemp[which(divetemp[,1]<3.5),1]+8.85804-10.14304,diverColl.35$richness,col="red")
points(divetemp[which(divetemp[,1]>10),1]-10.14304,diverColl.10$richness, col="blue", pch=3)
legend(8, 350, c("<3.5 Ma","3.5-10 Ma", "10-19.5 Ma"), cex=0.5, pch=c(1,2,3),
  col=c("red","black","blue"))
  ##ENDS

library(vegan)
data(BCI)
sp1 <- specaccum(BCI)
plot(sp1$sites,sp1$richness) #the plot assuming equal time bins
times <- c(1:5, 8, 22, 23, 25, 26:46, 56:65, 81:90)
plot(times,sp1$richness) #the plot with different time bins


##rarefaction
richness.80=rarefy(t(count.graham[,which(totalcount>80)]),80)
age.rar=age[which(totalcount>80)]
plot(richness.80,age.rar, ylim=c(20,0), xlim=c(0,45), xlab="number of species (rarefy cutoff=80)",
ylab="age(My)")##FIGURE RAREFACTION
abline(h=3.5)#
abline(h=10)#
text(40, 2, round(mean(richness.80[which(age.rar<3.5)],na.rm = TRUE),1),cex = .75)
text(40, 7, round(mean(richness.80[which(age.rar<10 & age.rar>3.5)],na.rm = TRUE),1),cex = .75)
text(40, 15, round(mean(richness.80[which(age.rar>10)],na.rm = TRUE),1),cex = .75)
##ENDS

t.test(richness.80[which(age.rar<10 & age.rar>3.5)],richness.80[which(age.rar>10)])
```

CHAPTER 9

BIOGEOGRAPHIC HISTORY OF *ABIES BRACTEATA* (D. DON) POIT. IN THE WESTERN UNITED STATES

Estella B. Leopold and Stephanie Zaborac-Reed*

ABSTRACT

Abies bracteata (D. Don) Poit., the Santa Lucia fir, is one of several conifers that are endemic along the west coast of California today, but with extensive fossil records indicating that they are "old" species, once more widely distributed in North America. Lineages of a number of these—namely, *Sequoia sempervirens* (D. Don) Endl., *Torreya californica* Torr., *Sequoiadendron* J. Buchholz, *Picea breweriana* S. Watson, and *Pinus balfouriana* Balf.—occurred together in the western United States during the Tertiary. The present paper is a search for the kinds of climatic or driving factors that brought about range displacement for one of these taxa, *A. bracteata*. We used pollen evidence in conjunction with megafossils from Rocky Mountain floras to demonstrate and evaluate the impacts of an abrupt climate degradation that occurred after 34 Ma at the beginning of the Oligocene. Our data indicate that by 26 Ma in Colorado, the mean annual temperature dropped about 6°C and summer precipitation declined. This cooling and drying followed extensive local volcanism, including the Fish Canyon Tuff of La Garita caldera (27.8 Ma), one of the largest known explosive eruptions. The cooling preceded a time of active uplift of the Colorado Plateau. Our data provide new insights into a highly debated subject: the regional extinction of taxa due to a complex of climate changes in Colorado during the Oligocene.

Key words: Megafossil, Oligocene cooling, pollen, range displacement.

Abies bracteata (D. Don) Poit., the Santa Lucia fir of California, is the rarest extant species of *Abies* Mill., and is the sole member of section *Bracteata* Engelm. Its home range today is limited to the mid elevations of the Santa Lucia Mountains of central coastal California. However, the megafossil record of *Abies* cf. *bracteata* is more widespread, occurring in the Eocene and Oligocene of Colorado, the Oligocene of Oregon, and the Miocene of Oregon, Nevada, and Idaho (Leopold & Zaborac-Reed, 2012), showing that this section was once widely distributed (Fig. 1).

Fossils of *Abies* cf. *bracteata* co-occur with several conifer taxa that grew together in the central Rocky Mountains during the Tertiary, but that are

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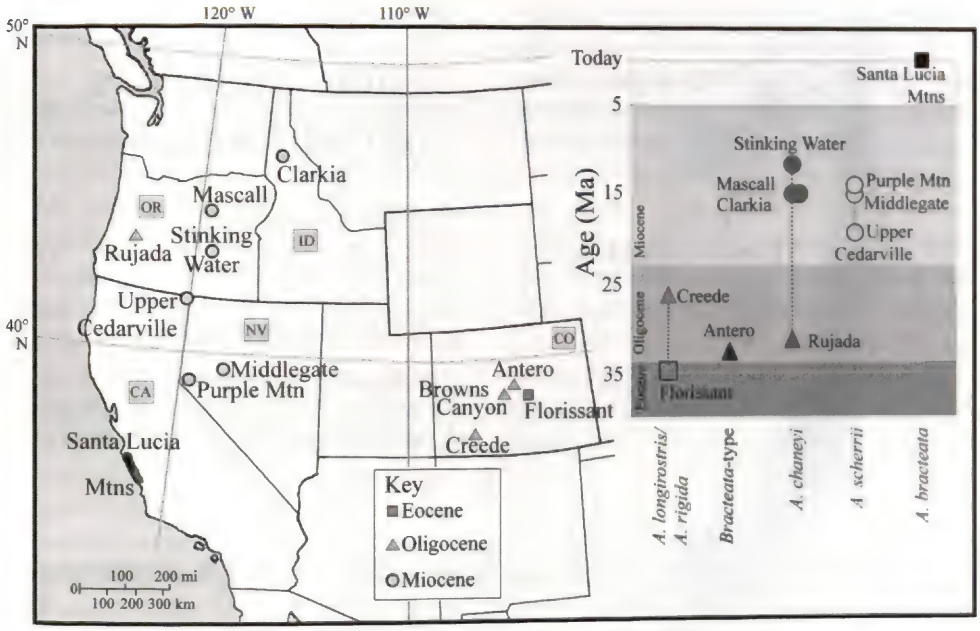


FIGURE 1. —Left. Map of fossil localities, western North America, identified by epoch. —Right. Species and ages of *Abies* sect. *Bracteata* members. Symbols for age of floras: squares = Eocene; triangles = Oligocene; circles = Miocene.

now endemic with disparate ranges along coastal California in areas that have a fairly equable climate (Table 1, Fig. 2). This biogeographic history, shared with *Sequoia* Endl., *Pinus* cf. *balfouriana* Balf., *Picea* cf. *breweriana* S. Watson, *Sequoiadendron* J. Buchholz, and *Torreya californica* Torr., represents a pattern of range displacement as outlined by Whittaker (1961).

The fossil records presented span the Eocene–Oligocene transition, a tumultuous period known from the marine record as a time when global temperatures decreased sharply (Zachos et al., 2001); it was a time when the opening of the Drake Passage permitted the development of the transantarctic current, and represented one of the most severe abrupt cooling periods of the Cenozoic,

TABLE 1. Climatic parameters for selected endemic conifers of California (after Thompson et al., 1999a). Notice that mean annual temperature (MAT) values overlap from 9°C to 11°C.

Endemic species	MAT (°C)	Range January temperature (°C)	Range July temperature (°C)	Annual precipitation (mm)
Sequoia	9–14	5–10	12–20	500–1200
Abies bracteata	9–14	6–8	12–19	500–1000
Torreya californica	9–15	1–9	12–25	500–1000
Sequoiadendron	8–16	–2 to 5	19–26	500–1100
Picea breweriana	5–11	–3 to 4	12–20	700–1200
Pinus balfouriana	3–11	–5 to 1	15–24	700–1200

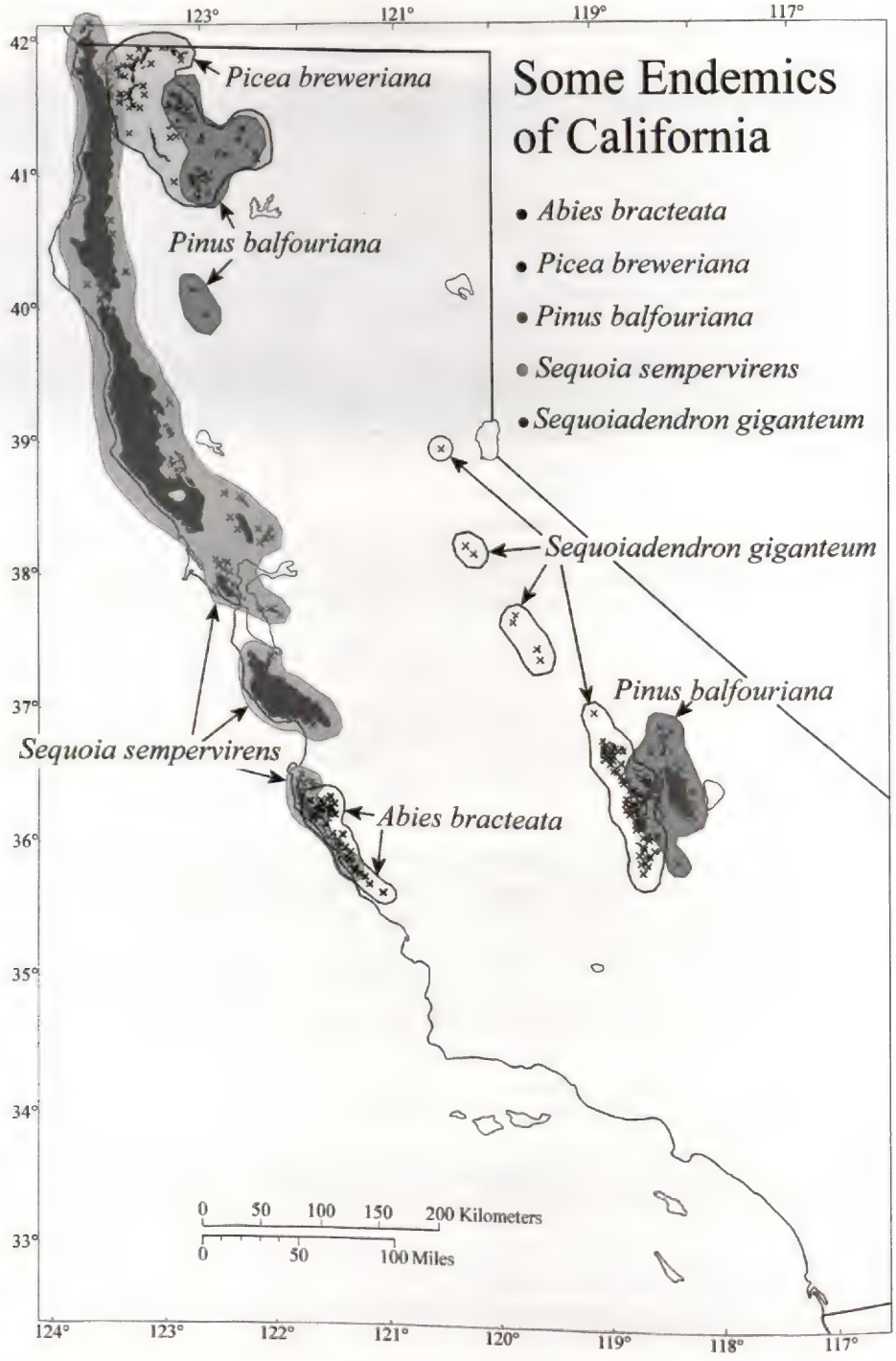


FIGURE 2. Some endemic conifers and their geographic ranges today in California (based on Griffin & Critchfield, 1972).

followed by a warming into the Miocene. Many floras of the world were impacted (Graham, 1999, 2012).

In the present paper, we augment information on the megafossil record of the lineage *Abies* sect. *Bracteata* described by Axelrod (1976, 1987) and others by providing new information about the corresponding fossil pollen, focusing on the Colorado floras.

We use a review of the megafossil record coupled with new evidence about pollen to explore the basis for the former and current distributions of a distinctive conifer. Our hypothesis is that the regional extinction of *Abies bracteata* in the western states was due to a complex of climatic changes. The thrust of the present paper is to identify the scale and direction of those shifts in climate.

Although this report is limited to the study of *Abies bracteata*, similar evidence can be brought to bear on the fossil history of other endemic conifers of California, such as *Sequoia*, *Sequoiadendron*, *Picea breweriana*, *Pinus balfouriana*, and *Torreya* Arn. These taxa have in common ancient origins (at least Eocene in age) and were widespread in western North America during the Eocene. Some of these taxa represent primitive elements within their genera, i.e., *A. bracteata* (Aguirre-Planter et al., 2012), *Picea breweriana* (Ran et al., 2006), and *Pinus balfouriana* (Lanner, 2007), while others are remnant taxa with only one or two living sister species (e.g., *Sequoia*, *Sequoiadendron*, *Torreya*). We hypothesize that because their ranges shrank westward from a mid-continent area formerly characterized by warm, moist summers to a cool, summer-dry climate with moderate winters, the main climatic shift probably involved a drop in both mean annual temperature and precipitation.

BACKGROUND

Species of *Abies* occupy coastal forests and mountain highlands of the Northern Hemisphere. The genus contains 48 to 55 species that are distributed in North and Central America, Europe, and Asia (GBIF, 2012). It is divided into 10 sections (nine are listed in Appendix 1), of which *A. bracteata* is the sole member of section *Bracteata* (Farjon & Rushforth, 1989).

Section *Bracteata* has been suggested as the most basal member of the genus based on its physical characteristics (Liu, 1971). Molecular phylogeny and phylogenetic studies of the genus show that *Abies bracteata* is genetically unique within the genus (Xiang et al., 2004; Aguirre-Planter et al., 2012); this work lends support to Liu's conclusion that it is indeed the most basal member of the genus.

ECOLOGY

Abies bracteata (the Santa Lucia fir or bristlecone fir) now grows in mixed evergreen forests between 200 and 1500 m (600–5100 feet) in elevation on the western slopes of the Santa Lucia Mountains of Monterey County, California, with most occurring above 1000 m (3200 feet). It grows sparsely in cool, wet canyons within 20 km (14 mi.) of the coast, and depends on the westerlies and fog belt from the Pacific Ocean for summer moisture (Ornduff, 1974). Its seedlings are extremely sensitive to drought, while the thin bark makes the mature tree vulnerable to fire damage (Axelrod, 1976). As a result, it grows where there is little risk of fire on slopes of 35°–40° (Talley, 1974). The present geographic range of the species is included on the maps in Figures 1 and 2. *Abies bracteata* occurs today in mixed conifer stands with certain broad-leaved sclerophylls that are also associated with endemic conifers along the West Coast (Talley, 1974; Axelrod, 1976).

Other conifer endemics along the west coast are of interest. The present range of *Picea breweriana* (Brewer's spruce) in the Klamath Mountains along the Oregon–California border is in dry highlands close to the coast (Thompson et al., 1999a). *Sequoia sempervirens* (D. Don) Endl. (coastal redwood) is endemic in the coastal ranges and fog belt of California. Both of these and *Abies*

bracteata are currently associated with *Arbutus menziesii* Pursh (madrone) and *Lithocarpus* Blume (tan oak), which are sclerophyllous hardwoods that have found refuge along the Pacific coast. *Sequoiadendron* (giant sequoia) is endemic at mid to high elevations in the western Sierra Nevada Range (Kings Canyon). *Pinus balfouriana* (foxtail pine) is endemic in high altitude areas of the western Sierra Nevada Mountains (Fig. 2). *Torreya* is found at higher elevations west of the Sierra Nevada mountain range and along the coast (Thompson et al., 1999a). Each now occupy areas of winter-wet climate, depending on humid Pacific westerlies for a source of moisture during the dry summers (Whittaker, 1961; Ornduff, 1974). All six of these conifers grow in relatively mild climate areas (mean annual temperature [MAT] overlapping at ca. 9°C–11°C; Fig. 3A). Figure 3 shows seasonal temperature ranges and precipitation requirements for six California endemics (overlap at 700–1000 mm for these taxa). The gray shaded vertical bars define the temperature and yearly precipitation niches that these taxa share today. They each formerly grew in climates that had somewhat higher summer precipitation, based on their associates. Each of these endemics were formerly widespread in the western United States and are examples of range displacement during the Middle and Late Tertiary (Chaney, 1948).

MORPHOLOGY

Abies bracteata has highly unusual female cones, on which slender spines (bristles) ca. 5 cm in

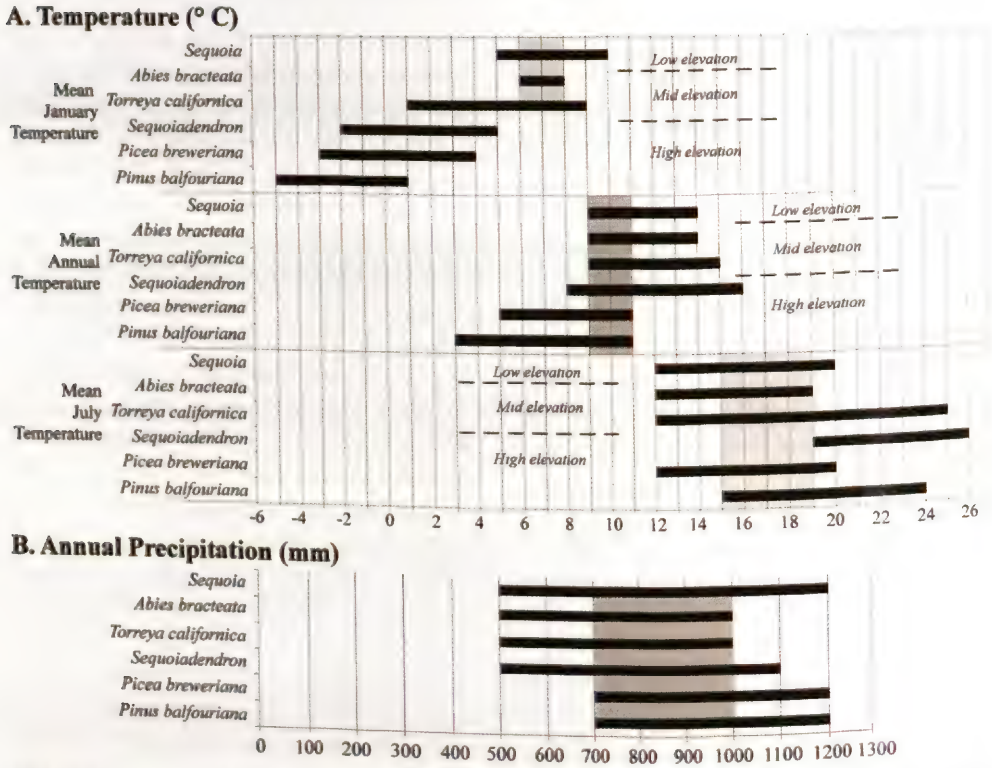

A. Temperature (° C)
Mean January Temperature
Mean Annual Temperature
Mean July Temperature
Sequoia
Abies bracteata
Torreya californica
Sequoiadendron
Picea breweriana
Pinus balfouriana
Low elevation
Mid elevation
High elevation
-6 -4 -2 0 2 4 6 8 10 12 14 16 18 20 22 24 26
B. Annual Precipitation (mm)
0 100 200 300 400 500 600 700 800 900 1000 1100 1200 1300

FIGURE 3. Environmental tolerances and conditions of some modern endemic conifers of California. —A. Temperature and elevation ranges. —B. Annual precipitation levels.

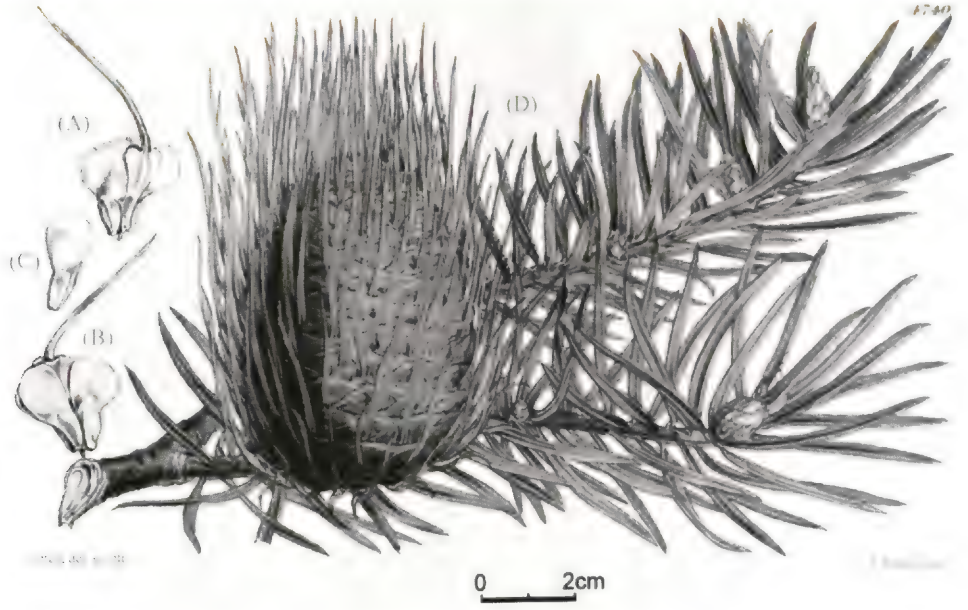


FIGURE 4. *Abies bracteata* of California (drawing reproduced from Hooker, 1853, plate 4740).

length extend up the bracts far beyond the cone scales, giving the cone a bushy look (Fig. 4). It is unique within the genus because it is the only species of *Abies* with this very long extension of bract scales beyond the cone scales. Most living *Abies* either lack substantive bracts on the cone scales, or have only smaller ones: some 13 out of 45 living species have bract tips that extend up to ca. 3 mm beyond the cone scale (Liu, 1971). The cone scales are wing shaped and about 2 cm in length. In addition, seeds have a flaglike wing, and long, flattened, acuminate (sharply pointed) needles reminiscent of *Torreya*.

FOSSIL RECORD

Megafossils. The oldest megafossil records of *Abies* in the Pacific Northwest occur at late Early Eocene sites in southern British Columbia and Washington in the Okanagan Highlands (Schorn & Wehr, 1986; Dillhoff et al., 2005; Greenwood et al., 2005). At these sites, *A. milleri* Schorn & Wehr has some of the characters of section *Bracteata*, though it lacks the long cone scale bracts.

The fossil record of section *Bracteata* extends from Late Eocene deposits in Colorado, including *Abies rigida* Knowlton in the Browns Canyon Formation (Upper Oligocene; Van Alstine & Cox, 1969), into Miocene records in Idaho, Nevada, and Oregon (Table 2, Fig. 1). In Colorado the earliest records occur in the Late Eocene Florissant Formation (34 Ma) where MacGinitie (1953) identified a well-preserved *Abies* seed with diagnostic wing shape as *A. longirostris* Knowlton and assigned it to section *Bracteata*.

The Oligocene records of the group are varied and have been given different names. In Colorado, cone scales and bracts virtually identical to those of modern *Abies bracteata* were found at Creede (26.5 Ma, Late Oligocene) (Fig. 5). Knowlton (1923) first described seed cone scales as *A. longirostris* Knowlton, and associated curled

A. rigida	Creede Flora, Colorado	—	Knowlton, 1923	—	—	—	—
		Late Oligocene, 26.5	Axelrod, 1987	11.5	460–635; adequate summer precip.	1600	2700
		Late Oligocene, 27.2	Wolfe & Schorn, 1989	< 2.5	635; dry summers	ca. 2500	2700
			this report	ca. 9	dry summers	—	—
A. rigida	Browns Canyon Formation, Colorado	Oligocene	Van Alstine and Cox, 1969	—	—	—	—
A. chaneyi	Rujada Flora, Oregon	—	Lakhanpal, 1958	—	rainfall through the year; wet summers	—	1000
		Early Oligocene, 31.5	Prothero, 2008	13.0			
Bracteata-type pollen	Antero Flora, Colorado	Early Oligocene, 33.8	Meyer et al., 2012	—	dry summers	—	—
			this report	12.7		—	ca. 2773
A. longirostris	Florissant Flora, Colorado	—	MacGinitie, 1953	ca. 18; hot summers	> 600	< 914	2500
			Boyle et al., 2008	14.7–15.6	500; moist summers	—	—
			Leopold & Clay-Poole, 2001	17–18	> 800; moist summers	< 914	2500
			this report	17	—	—	—
		Late Eocene, 34.07	Evanoff et al., 2001	—	—	—	—

Abbreviations: MAT = mean annual temperature; precip. = precipitation.

TABLE 2. List of *Abies* sect. *Bracteata* fossil taxa by age, showing location and estimated environmental conditions by various authors.

Abies species	Location	Age (Ma)	Source	Estimated MAT (°C)	Estimated annual precip. (mm)	Estimated paleo elevation (m)	Estimated modern elevation (m)
Abies bracteata	Santa Lucia Mountains, California	Modern	Sullivan, 1993 Talley, 1974	9–14	500–1200	—	180–1300
A. chaneyi	Stinking Water Flora, Oregon	—	Chaney & Axelrod, 1959	—	—	—	—
		Late Miocene, 12.1	Evernden & James, 1964				
A. scherrii	Purple Mountain Flora, Nevada	Middle Miocene, 14.8	Axelrod, 1976, 1995	11.5	760–880; some summer precip.	1338	728
A. scherrii	Middlegate Flora, Nevada	—	Axelrod, 1976, 1985	12	760–890; some summer precip.	1670	1500
		Middle Miocene, 15.9	Evernden & James, 1964	—	—	—	—
A. scherrii	Upper Cedarville Flora, Nevada	—	LaMotte, 1936	—	—	—	—
		19.8	Evernden & James, 1964				
A. chaneyi	Mascall Formation, Oregon	Middle Miocene	Mason, 1927 Chaney & Axelrod, 1959 Axelrod, 1976	—	—	—	—
		15.4	Evernden et al., 1964				
A. chaneyi	Clarkia Flora, Idaho	Middle Miocene, 22, 15.3, 12.8	Smiley & Rember, 1985	14–18	summer precip.	—	—
		15	Denk et al., 2011	—	—	—	—

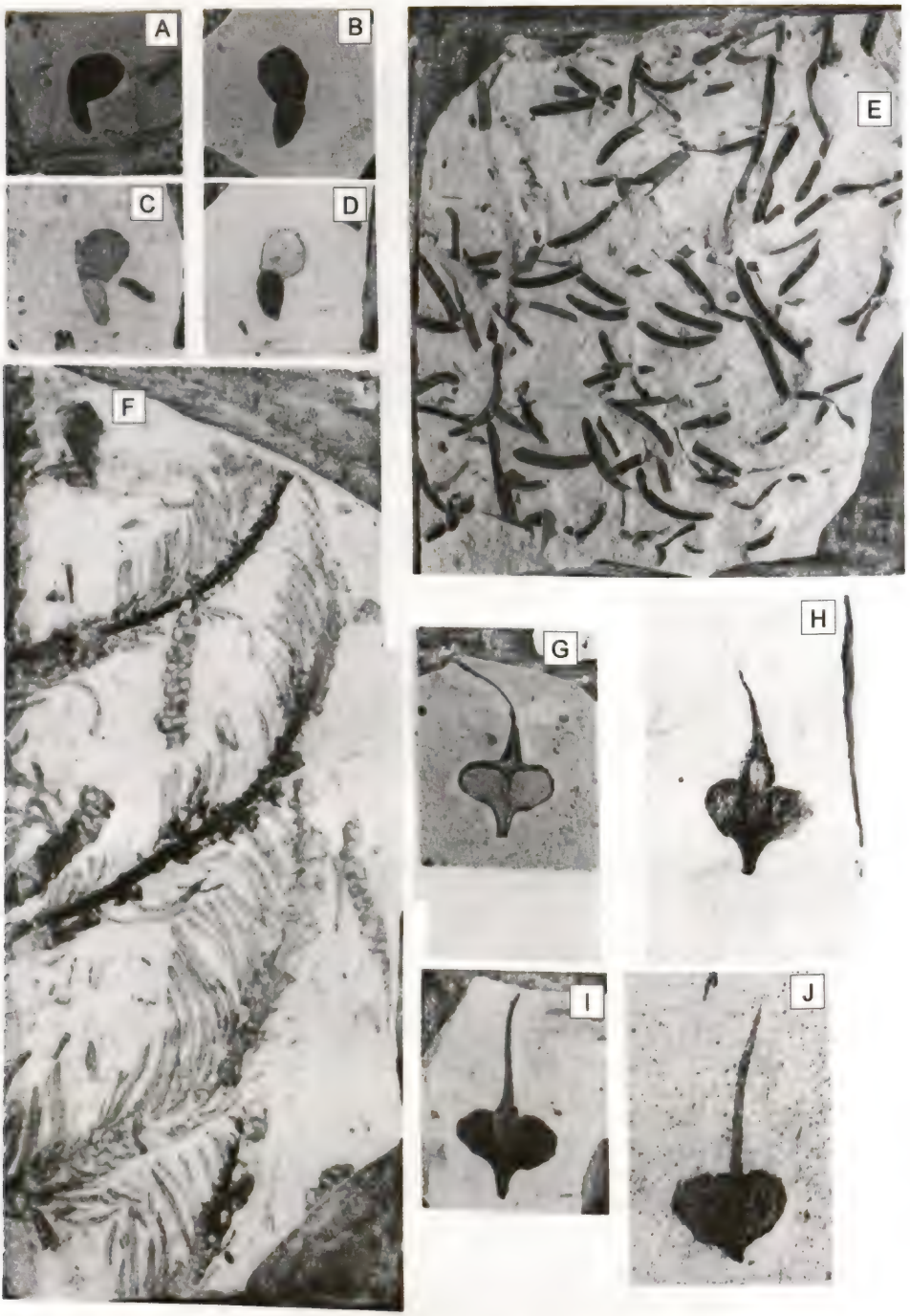


FIGURE 5. Fossil *Abies rigida* remains. A–D. Seeds. —E. Loose needles. —F. Branch tips. G–J. Cone bracts with characteristically long spines. Reprinted from plate 6 of *The Late Oligocene Creede Flora, Colorado*, by Daniel I. Axelrod, © 1987 by the Regents of the University of California. Published by the University of California Press.

needles as *A. rigida* (Fig. 5). Megafossils of *A. rigida* are also reported from the Browns Canyon Formation (Oligocene; Van Alstine & Cox, 1969). Later Axelrod (1987) redescribed similar fossil needles, along with associated stems and bracts from Creede, and placed them all in *A. rigida*. At Creede sites, diverse cone scales, seeds, and needles of the group were present or common at two of the sites and rare or absent at the other two (Axelrod, 1987).

In eastern Oregon, Mason (1927) described needles, scales, and a seed from the Miocene Mascall flora that he related to *Abies bracteata* based on morphology and named *A. chaneyi* Mason. Cone scales and bracts of *A. chaneyi* were found at the Oligocene Rujada flora (31.5 Ma) of western Oregon (Lakhanpal, 1958), as well as at the Miocene sites of Stinking Water, Oregon (Chaney & Axelrod, 1959), and Clarkia, Idaho (Denk et al., 2011; Table 2). The Miocene fossil sites in Nevada include the Middlegate and Purple Mountain floras, where Axelrod (1985, 1995) described rarely occurring cone scales very similar to those of *A. bracteata*; these remains, with long, tapering bracts extending 4 cm beyond the cone scale, he named *A. scherrii* Axelrod. A specimen was also reported from Upper Cedarville, Nevada (LaMotte, 1936; Table 2). These cone scales and bracts are very similar to the remains at Mascall.

Fossil pollen. In western North America, identifiable pollen of some Pinaceae genera first appear close to the Paleocene/Eocene transition, including *Picea* A. Dietr. and *Tsuga* Carrière (Leopold & MacGinitie, 1972). Among these is the genus *Abies*; its pollen record begins in the lower sediments of the Eocene Golden Valley Formation in the Williston Basin of North Dakota (Hickey, 1977: 89–90). Dillhoff et al. (2005) found *Abies* pollen in the early Middle Eocene McAbee Formation of British Columbia. Leopold and Clay-Poole (2001) reported fossil pollen of *Abies* cf. *bracteata* at Florissant, while *A. bracteata*-type remains are also reported at the Browns Canyon Formation in Colorado (Van Alstine & Cox, 1969). Leopold also reported *Abies* cf. *venusta* (Douglas) K. Koch (syn. *A. bracteata*) at Platoro Caldera (USGS D4772), 29 Ma, in Lipman (1975).

MATERIALS AND METHODS

We studied modern reference pollen slides from 13 *Abies* taxa and utilized existing published records and photographs of *Abies* pollen types (including 14 additional species; see Appendix 1). The modern reference collections Leopold made at the United States Geological Survey Denver Laboratory and the Jane Gray pollen collection now at the Burke Museum of Natural History and Culture, University of Washington, are the basis for the pollen study (Appendix 1). The modern reference materials had been prepared with acetolysis, mounted in glycerin jelly onto slides, and the cover slips sealed (Fægri et al., 1989).

We measured the size of these grains and calculated standard deviations in an effort to discern what parameters may be diagnostic of section *Bracteata* pollen grains. The sample included 13 species, with 10 to 21 grains measured for each collection. We measured the thickness of the cappus wall, especially distal from the pole, since many *Abies* taxa show thinning of the cappus wall at the pole itself (see Appendix 2).

In order to determine the presence of pollen morphotypes of *Abies bracteata*, we studied fossil pollen from three Paleogene floras of Colorado. The latest Eocene Florissant Formation (34.2 Ma) of central Colorado has a highly diverse megafossil flora dominated by hardwoods (MacGinitie, 1953). More limited Oligocene floras from the same area are the younger Antero Formation (about 10 km distant, dated at 33.8 Ma) (Durden, 1966; Meyer et al., 2012) and the Creede Formation of southwestern Colorado (26.5 Ma; Axelrod, 1987). Table 2 summarizes the inferred paleoclimate data from various authors. For purposes of recording present-day environmental parameters where modern relatives of the Oligocene genera grow today, we assembled climatic data in Table 3.

TABLE 3. Mean annual temperature (MAT) ranges today of certain taxa that have records in Oligocene floras of the western United States (based on Thompson et al., 1999a, 1999b).

Taxa	MAT range (°C)	MAT (°C)
Abies bracteata (D. Don) Poit	9 to 14	11.5
Picea breweriana S. Watson	5 to 11	8
Podocarpus L'Hér. ex Pers. + (Mexico)	—	ca. 14‡
Tsuga Carrière*	–3 to 13	6
Betula L.*	–5 to 20	7.5
Cercocarpus Kunth (e.g., *C. breviflorus* A. Gray)	5 to 20	13.5
Populus L. (e.g., *P. fremonti* S. Watson)	3 to 25	14
Prunus L.	0 to 26	13
Quercus L. (western)*	–4 to 26	9
Shepherdia Nutt.*	–2 to 12	6
Ulmus L., Ulmoideae†	–2 to 22	10

*Genera removed from Creede flora by Wolfe and Schorn (1989, 1990); reinstated at Creede by pollen evidence (this report).
†Identified by pollen at Creede.
‡P. S. Martin, unpublished.

We also reviewed the literature for the presence of *Abies bracteata*-type megafossils, and made note of the growth habits and environmental requirements of the modern fir in the Santa Lucia Mountains of California.

RESULTS

Because of the clear identification of section *Bracteata* in the megafossil records in four Paleogene Rocky Mountain sites, we made an effort to diagnose the *Abies bracteata* pollen morphotype in the fossil pollen assemblages. Criteria for identifying and discriminating among other pinaceous genera by their pollen profiles are summarized in Figure 6 and discussed below.

We were concerned about possible overlap in morphology with other genera in the Pinaceae (Bagnell, 1975). Pollen of *Pseudolarix* Gordon is two-bladdered and very similar to that of *Pinus* but half its size. Both *Keteleeria* Carrière and *Pseudolarix* typically tend to have relatively large bladders that extend equatorially well beyond the pollen cell width in the equatorial plane (Fig. 6; Wang et al., 1995); the pollen often look alike except for the overall size. Minor elements in the Creede pollen flora include possible *Cathaya* Chun & Kuang, which can be confused with small pine (Sivak, 1977; Wang et al., 1995), and *Podocarpus* L'Hér. ex Pers., which differ by having oversize bladders and a dense, robust central cell (Ueno, 1958; Sivak, 1977; Pocknall, 1981; Wang et al., 1995; Liu & Basinger, 2000). While Cenozoic megafossils of *Podocarpus* are extremely rare in the western United States (Reinink-Smith & Leopold, 2005), *Podocarpoxylon* Gothan wood was tentatively identified from a log 12 inches in diameter by R. A. Scott in a Late Eocene unit of central Colorado (the same age as the Florissant Formation; Van Alstine & Cox, 1969). A recent finding by Kvaček and Rember (2000) identified the cuticle of the Asian conifer *Cathaya* in the Miocene of Clarkia, Idaho, which may be the youngest report of it in the United States.

Of particular concern is *Keteleeria* pollen, which is of large size and similar in shape to *Abies*. Based on an array of modern reference slides and a careful study by Zanni and Ravazzi (2007), we identified *Keteleeria*-type pollen as separate from *Abies* pollen by the following features: the cappus wall is thin and of even thickness, and the distal area of the leptoma (near the aperture) is decorated with inward-leaning verrucae ("warts"). In contrast, *Abies* has a thick, robust cappus wall of uneven thickness and a smooth leptoma near the aperture. Figure 7 photographs compare modern pollen of *A. bracteata* and *K. davidiana* (Bertrand) Beissn. Sun et al. (1980) described an Oligocene association of *Keteleeria* and *Abies* from Shaanxi Province, China, and their figured specimens closely resemble those in our Paleogene material. Note that *Keteleeria* megafossils have been found in the Oligocene of Oregon and the Mio-

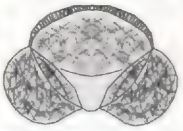
***Genus* / Size (µm)**	**Pollen**	***Genus* / Size (µm)**	**Pollen**
Abies 75 – 205		*Picea* 110 – 150	
Keteleeria 110 – 190		*Pinus* 50 – 110	
Cedrus 70		*Pseudolarix* 68	

FIGURE 6. Pollen profiles of different Pinaceous genera.

cene of the Latah flora, Washington (LaMotte, 1952).

The basic features of *Abies* pollen (Fig. 8A) include the following: the robust cappus wall (with its typical thinning at the pole and very distinct columellae in the cappus wall); the coarseness of the bladder reticulum (this distinguishes pollen of *Abies* from pollen of *Picea*, which generally has a fine reticulum); the oblong to round shape of the pollen cell; the junction of the reticulum, which grades into the main cell gradually; and the acute angle where the bladder meets the cell (in the equatorial profile view of *Picea* this is an obtuse angle).

As a result, it is generally easy to distinguish *Abies* from similar members of Pinaceae.

Within the genus *Abies* we found that the ratio of equatorial to polar (Eq/P) dimensions proved to be the best way to discriminate between pollen of *A. bracteata* and that of other living *Abies*. Figure 9A and Appendix 2 show the range (SD) and average measurements of the Eq/P ratio. While there is some overlap between some species, the average ratio of Eq/P dimensions in *A. bracteata* is 1.21:1. The body of the *A. bracteata* grain along the polar axis is almost as long as the equator; this gives the cell body a rounded look. The average ratio of Eq/P dimensions in the other species studied range from 1.29:1 to 1.57:1, resulting in a cell body with a visibly oblong shape by comparison.

The thickness of the cappus wall is an important distinguishing feature. *Abies bracteata* has a thick cappus wall, frequently thinning at the proximal pole. In that case the cappus wall thickens just halfway between the pole and equator, and is on average 9.9 µm thick. Only one other species studied has a cappus wall that is consistently thicker: *A. cephalonica* Loudon, the Greek fir. We found that the other taxa have thinner cappus walls (Fig. 9B).

In overall size *Abies bracteata* pollen is relatively large, though not the largest in the genus (Fig. 8B–E; Appendix 2). The pollen of *A. bracteata* averages 169.07 µm in length (in 18 specimens),

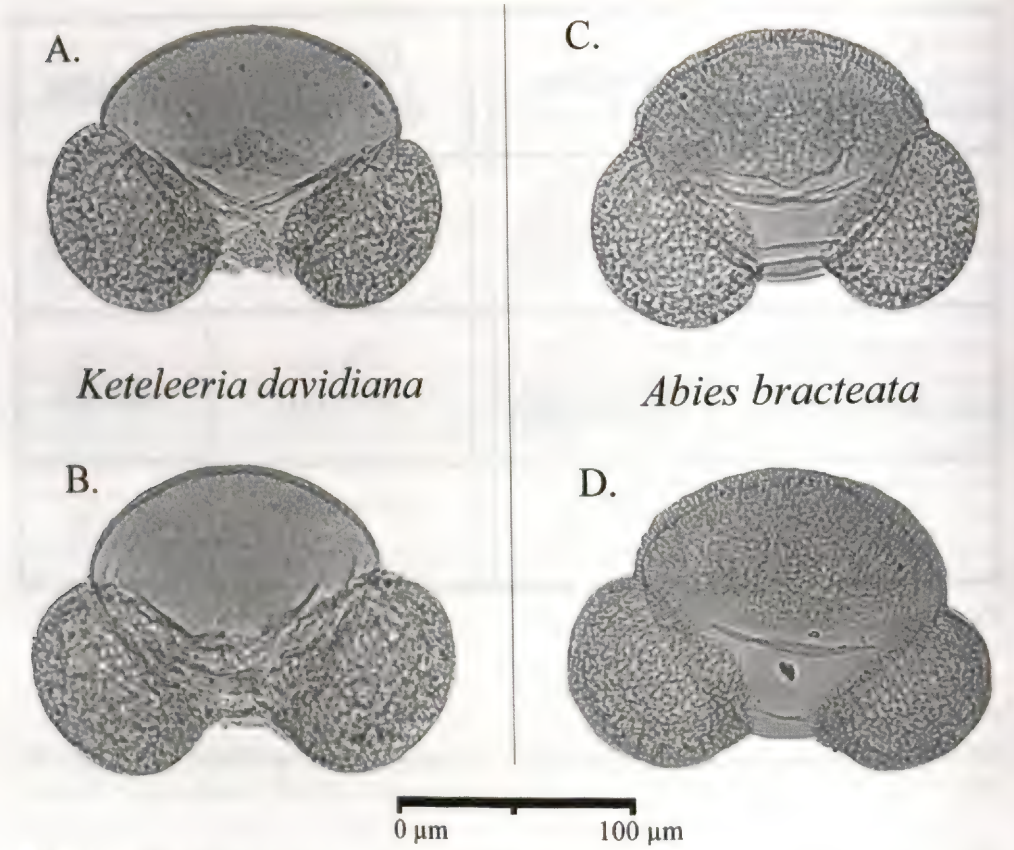


FIGURE 7. Distinguishing pollen of *Abies* and *Keteleeria* (modern samples).—A. *Keteleeria davidiana*, 167 µm. Slide JG 7.1.71.—B. *Keteleeria davidiana*, 180 µm. Note the verrucae along the aperture. Slide JG 7.1.61.—C. *Abies bracteata*, 158 µm. Slide 226.—D. *Abies bracteata*, 174 µm. Note the smooth leptoma area along the aperture. Slide S226.

while four other species have larger pollen (*A. mariesii* Mast., *A. magnifica* A. Murray bis, *A. balsamea* (L.) Mill., and *A. procera* Rehder). Nine others are smaller; the smallest, *A. veitchii* Lindl., averages only 83.73 µm in length.

No other *Abies* pollen meet these three criteria when taken together (small Eq/P ratio, very thick cappus, and relatively large size), allowing us to have confidence in the identification of the *A. bracteata*-type pollen in the fossil record.

The section *Bracteata* pollen morphotype appears to be present in the Florissant, Antero, and Creede formations (modern and fossil photographs in Fig. 10), as well as in the Browns Canyon Formation (Van Alstine & Cox, 1969), where, except for Antero, the pollen type is associated with megafossils of section *Bracteata*. Though there are many intermediate forms, we feel this appraisal is strongly suggestive of section *Bracteata* pollen in these fossil beds. Previously, we identified pollen of *Abies* cf. *bracteata* at Florissant (Leopold & Clay-Poole, 2001) correctly in plate 4, fig. 1, but the specimen in plate 3, fig. 2 is only assignable to *Abies* rather than to *A. bracteata*. Although specimens from Antero are smaller in size, this material is mounted in plastic; pollen grains mounted in plastic are generally smaller, here by about 12% smaller than material mounted in glycerin jelly

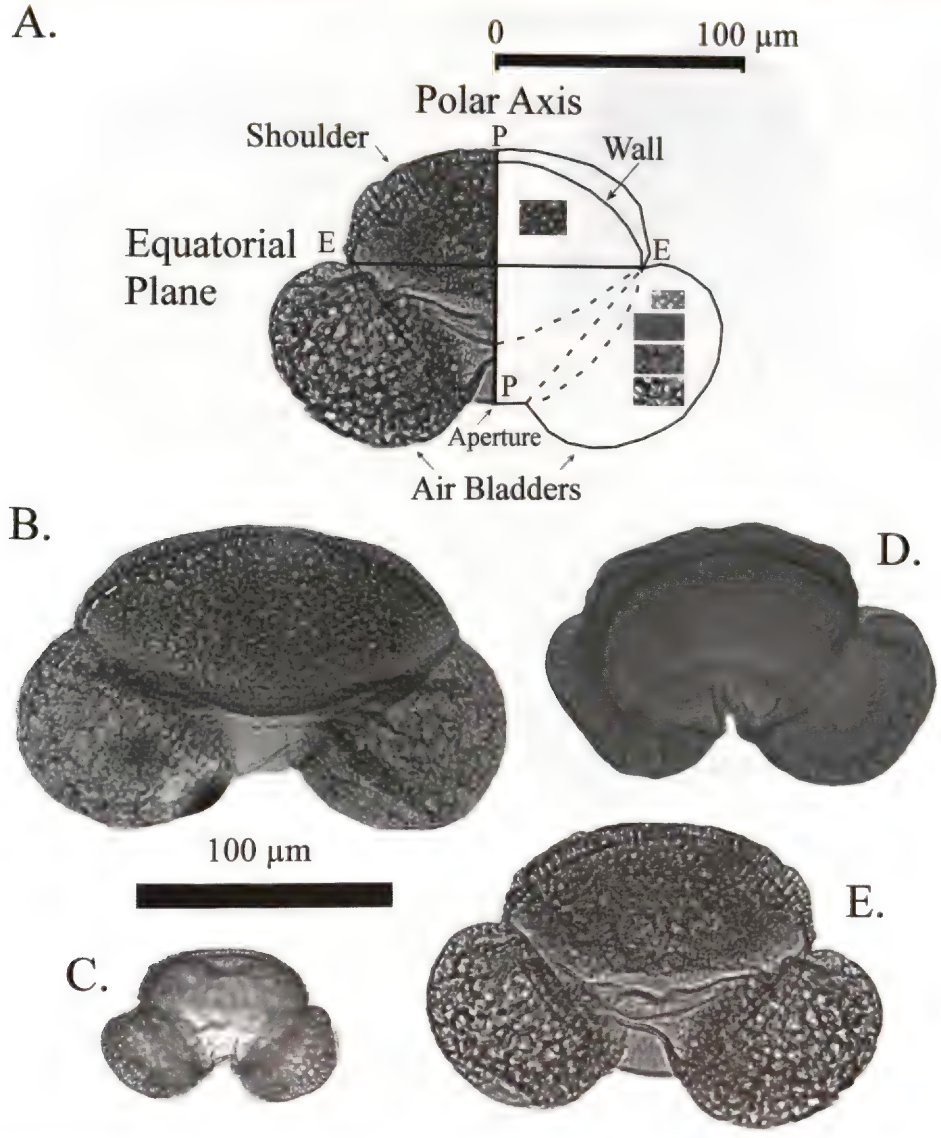


FIGURE 8. *Abies* pollen. —A. Characteristics of *Abies* pollen. B–E. Photographs of modern *Abies* pollen. —B. *Abies mariesii*, 196 µm. Slide JG 6.28.61. —C. *Abies veitchii*, 83 µm. Slide JG 1.62. —D. *Abies cephalonica*, 144 µm. Slide 2100. —E. *Abies bracteata*, 185 µm. Slide JG 12.11.55.

(see Moore & Webb, 1978). The Eq/P ratio and thick cappus give us confidence that we have positively identified *A. bracteata*-type pollen at Antero.

At each of the three Colorado pollen sites studied herein, two to four samples were counted. The broad changes in composition are delineated in Figure 11 (see Appendix 3). At Florissant the dominant forms in two samples are "Taxodiaceae/Cupressaceae/Taxaceae" ("TCT") pollen (Taxodiaceae-type, 65%) and in a third sample broad-

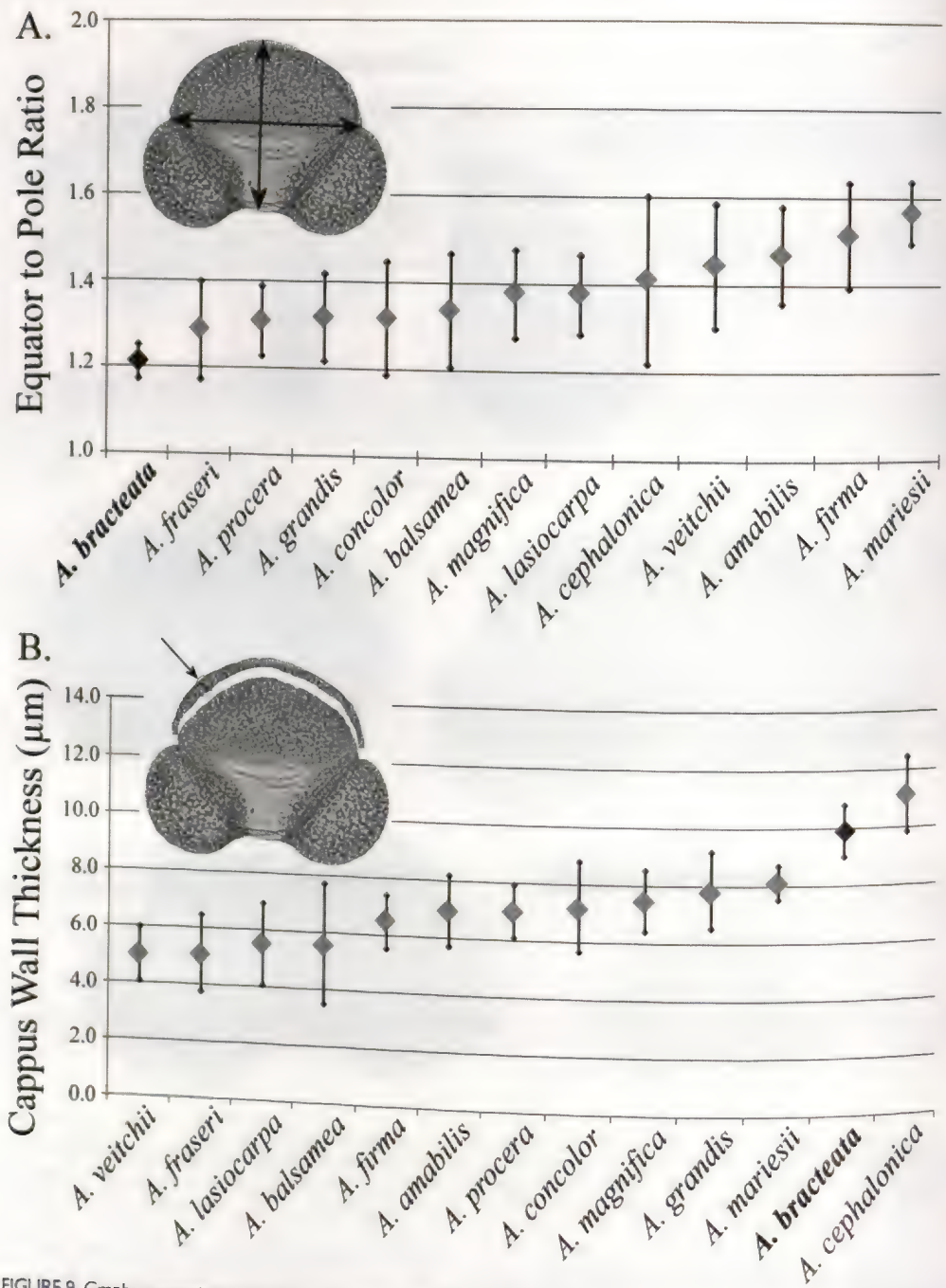


FIGURE 9. Graphs comparing results of modern *Abies* pollen measurements among several species; bars indicate standard deviations. —A. Equator to pole (Eq/P) ratio. —B. Cappus wall thickness (µm).

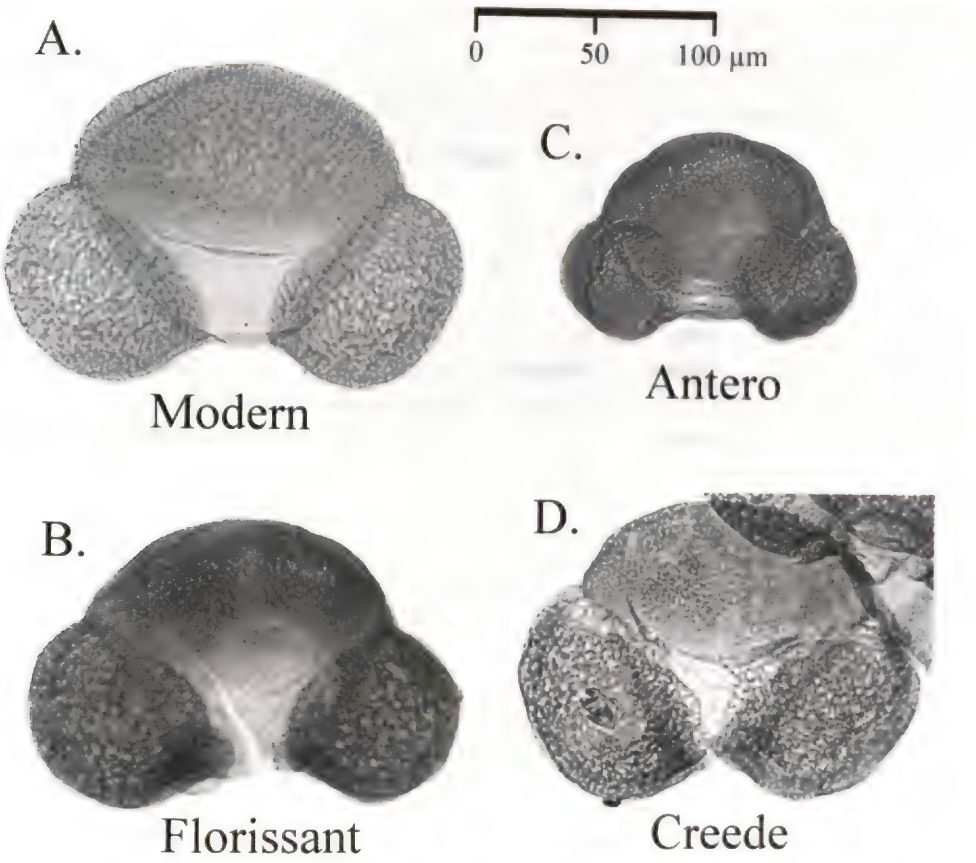


FIGURE 10. Photos of *Abies bracteata*-type pollen in three floras. —A. Modern *A. bracteata*, 184 µm. Slide UW S226. —B. Fossil, 173 µm. Florissant slide, D1083* (1). —C. Fossil, 123 µm. Antero slide, University of Colorado R2063-3. —D. Fossil, 167 µm. Creede slide, D1181-18*. * = U.S.G.S. Paleobot. Loc. No.

leaved tree types (52%) dominate. Pollen of the genus *Abies* is rare (1%–4% of the total pollen count). *Keteleeria* types were absent and *Podocarpus* types were minor elements (< 1%). The results of our pollen counts appear in Figure 11, including three samples at Florissant, two at Antero, and four at Creede. At Florissant, the results for two of the pollen counts are similar to samples published by Wingate and Nichols (2001) of land flora from the middle shale unit D7012, showing a dominance of "TCT" pollen, suggesting the *Sequoia* grove area. A third Florissant sample (D1496) shows the typical dominance of hardwood taxa at Florissant, also shown in Leopold and Clay-Poole's (2001; loc. W1) pollen work.

At Antero the collections of megafossils constitute a small dicot flora with several gymnosperm taxa (Durden, 1966; Barton, 2010). Unlike Florissant, the Antero pollen samples are dominated by Pinaceae (57% and 80%), and broad-leaved trees represent only 11%–18% of the count. *Picea* (ca. 7% and 35%) and *Pinus* (ca. 31% and 25%) are the most abundant pollen genera. A very small *Pinus*-type pollen (ca. 60 µm) may be that of *Pseudolarix* and/or *Cathaya* (ca. 2% and 6%). *Podocarpus* is a regular minor element (ca. 1%).

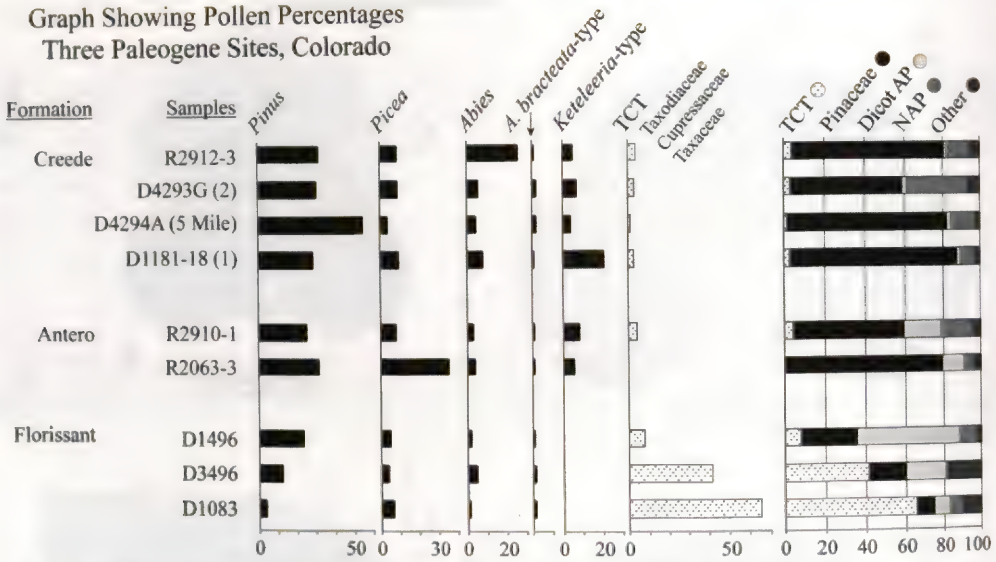


FIGURE 11. Percent total pollen counts for samples of three Paleogene units in Colorado. Percent dicot arboreal pollen (Dicot AP) represents the declining importance of hardwoods in the Paleogene samples. Non-arboreal pollen (NAP, or non-tree) taxa rise in importance in certain Creede samples.

In our Antero samples, *Abies* is uncommon (3% and 2%), and only 0.3% and 0.6% of the total count are of the *A. bracteata* pollen type. Pollen of *Keteleeria*-type is occasional (5% and 8%).

The preservation of the fossil pollen at Creede is relatively poor in most of our 15 samples. Three of the best Creede samples were counted (tallies 500 grains). Pinaceae are prominent (ca. 58%–86%), while nontree shrubs (7%–31%) greatly outnumber broad-leaved tree taxa (ca. 1%). Amongst the Abietineae pollen, *Keteleeria*-type is about as common (3%–20%) as *Abies* (4%–25%). The number of specimens of *A. bracteata*-type pollen is fairly low (0.3%–1.8%). Even at the Five Mile Bridge locality (D4294A) where *A. rigida* represents 36% of the megafossils listed by Axelrod (1987), the pollen representation of the section *Bracteata* morphotype is only trace (1.8%). The relative rarity of *Abies* cf. *bracteata*-type pollen may be partly due to the need to find specimens in the exact equatorial plane orientation in order to obtain the ratio of equator to pole dimensions and obtain measurements of the cappus wall. At Creede, *Podocarpus* represented a trace (0.6%–1.6%) element and *Ephedra* L. pollen is common. Dicot genera are chiefly dryland shrubs (e.g., *Sarcobatus* Nees, *Artemisia* L.) and riparian taxa. The pollen data generally confirm the increased dominance of conifer taxa at Creede and the paucity and infrequency of hardwoods.

Comparing the plant evidence from three formations, the main changes after the Late Eocene Florissant flora at 34 Ma through the Oligocene in Colorado are severe loss of hardwoods and progressive dominance of conifers.

DISCUSSION

REVIEWING THE FOSSIL OCCURRENCE OF *ABIES* CF. *BRACTEATA* LINEAGE

Megafossil records for 10 floras in the western United States contain remains of *Abies* sect. *Bracteata* (Table 2). The most abundant remains (*A. rigida*) are found at Creede at the Five Mile Bridge

locality. The floristic data for the Creede Formation present conflicting accounts by Wolfe and Schorn (1989) and an earlier publication by Axelrod (1987). These authors did not agree on the diversity of the floras or on the type of climate represented.

The morphological sequence of megafossil findings of section *Bracteata* are portrayed as sketches of the fossil organs (Fig. 12), showing the fossil types in ascending order by age. The fossil cone scales of *Abies* cover a range of forms, but the most singular is the ear-shaped cone scale and attached bract at the Creede flora (*A. rigida)* that so strongly resembles that of *A. bracteata* (compare Figs. 4, 5). The fossil shows a long, linear bract extending beyond the cone scale by 2.5–5 cm. The bract at the base is bilobate. Present also at Creede are diverse remains such as curved needles (brush-like), winged seeds up to 1.5 cm long, and pollen. These remains are common. They are associated with other conifers and remains of *Pinus crossii* Knowlton, thought to be an ancestor of *P. aristata* Engelm. (bristlecone pine). Axelrod thought that the lack of attenuated lobes on the cone scale bract implied that *A. rigida* was not a close relative of *A. bracteata*—perhaps more closely related to the Asian *A. georgei* Orr. However, Wolfe and Schorn (1989) argued that the long bract and other features placed it in section *Bracteata*, and claimed *A. rigida* was an extinct sister

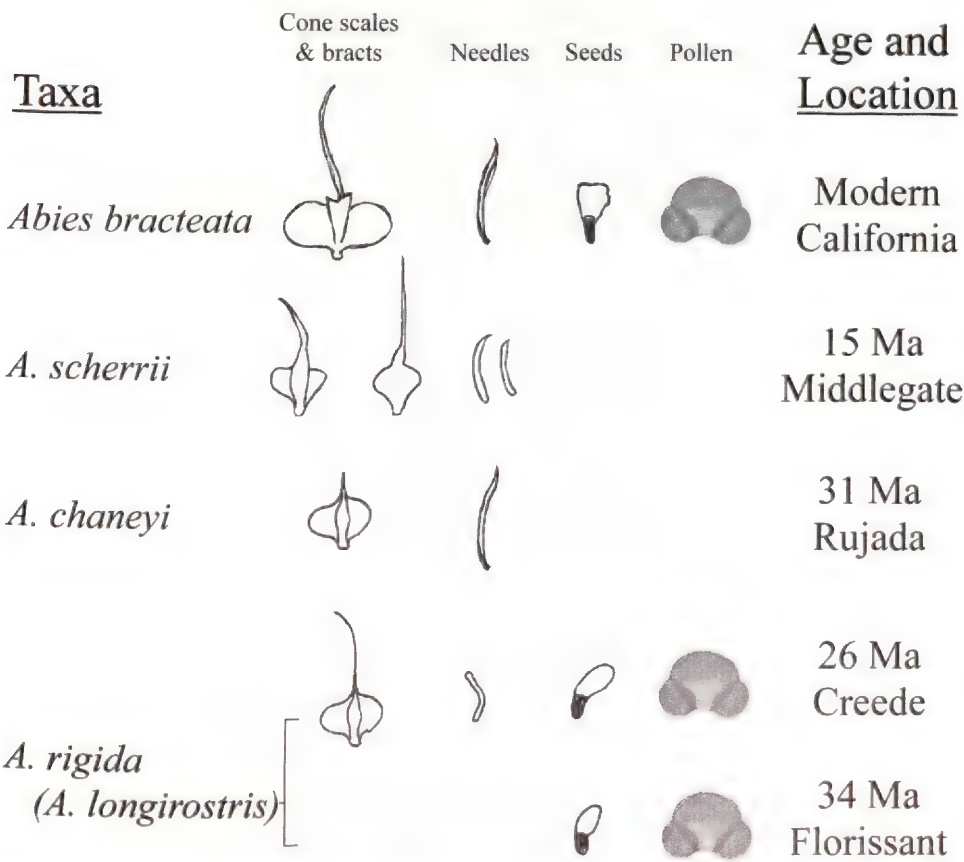


FIGURE 12. Synthesis of the chronology of *Abies* sect. *Bracteata* megafossil types in the Tertiary record.

lineage of *A. bracteata*. We accept their observation based on the great similarity of *A. rigida* with the unique *A. bracteata*. Wolfe and Schorn (1989) considered the curved, brush-like needles (as in *P. crossii)* an adaptation related to heavy snowfall conditions. A cone scale was identified as *Abies* cf. *rigida* in Meyer's (2012) Red Rock, New Mexico, flora but appears to lack the characteristic long bract of the Santa Lucia fir.

At Florissant (Latest Eocene), MacGinitie assigned a fossil *Abies* seed to *A. longirostris* (later reclassified as *A. rigida*) as "a close relative of *A. bracteata*" (MacGinitie, 1953: 82). *Abies* cf. *bracteata* pollen is also present (Leopold & Clay-Poole, 2001). The conditions at Florissant were clearly warm, which may be the reason that megafossil remains of the "montane" *A. rigida* are rare at Florissant.

A flora in the immediate vicinity of Florissant but less than one million years younger is the Antero flora (Early Oligocene) described by Durden (1966). Though vegetative remains of *Abies* cf. *bracteata* were not found here, we do record the presence of good morphotypes of section *Bracteata* pollen (Fig. 10).

Younger sites, such as the Middlegate and Purple Mountain floras of Nevada (Middle Miocene), include remarkable cone scales and bracts much like those found at Creede; Axelrod (1985, 1995) named these *Abies scherrii* Axelrod. Fossil needles are also present. The Purple Mountain flora has a strong representation of mixed evergreen and hardwood forest with diverse woody, deciduous dicots. Winged seeds and curved needles are also present in the Middlegate flora (Axelrod, 1976). Section *Bracteata*-type cone scales and needles also appear in the Oligocene Rujada flora of Oregon as well, identified as *A. chaneyi* Mason (Lakhanpal, 1958).

CLIMATIC FACTORS AND THE OCCURRENCE OF ENDEMIC GENERA

Taking the biogeographic and climatic information from six endemic conifers now living in California, it is possible to define the climatic thresholds that limit the mixed evergreen and conifer forests where these taxa grow today. Figure 3 demonstrates that all six have in common a relatively equable climate defined by their mean annual and range of seasonal temperatures. All of them seem to share a tolerance for hot, dry summers. Clearly the higher-elevation taxa (e.g., *Pinus balfouriana*, *Picea breweriana*, and *Sequoiadendron*) are more tolerant of cool winters (down to –5°C, –3°C, and –2°C, respectively) than the low- to mid-elevation endemic conifers *Torreya*, *Sequoia*, and *Abies bracteata* (Fig. 3). Using the climatic data from Thompson et al. (1999a, 1999b), the mean annual temperature for *A. bracteata* and other low- to mid-elevation endemic conifers today is very much in the same range: 9°C–14°C MAT. Precipitation for the *A. bracteata*/evergreen forest association is ca. 500–1000 mm annually with dry summers. For the cold-month temperatures, *A. bracteata* and *Sequoia* are alike, but *Torreya* ranges down to near 0°C. Relatives of these three endemic conifers grew in the Florissant area at the end of the Eocene.

The following three floras of Paleogene age are each set in an active volcanic landscape with frequent ash falls.

Florissant Formation. The Florissant fossil flora is highly diverse, having as many as 67 megafossil genera and around 150 pollen and spore types, which together imply a warm climate. The megafossil flora is dominated by arboreal hardwoods, and gymnosperms are of small numerical importance except for in the *Sequoia* forest facies in the southwest corner of the valley bottom. Endemic conifers include *Sequoia* and *Torreya*. The rarity of *Abies* cf. *bracteata* fossils suggests that it grew on slopes above the valley bottom.

At Florissant, Boyle et al. (2008) compared fossil taxa with analogues among living forest floras and inferred a mean annual temperature of the Florissant flora to be between 14.5°C and ca. 15.6°C. They stated that the flora verges on a

subtropical to warm temperate climate. We have averaged this to 15°C. Based on the nearest living relatives and taking into account the various tropical insects found at the site, MacGinitie (1953) suggested a MAT of 18°C for taxa growing along the valley bottom. Leopold and Clay-Poole (2001) suggested a MAT of 17°C–18°C. Wolfe and Schorn (1989) suggested that precipitation was around 635 mm, with dry summers.

Antero Formation. The flora of the Antero Formation (Durden, 1966) is very sparse (14 megafossil genera including *Sequoia,* and 21 pollen genera) and suggests a cool temperate climate. Antero shares a number of features with the slightly younger, nearby Pitch-Pinnacle flora of Gregory and McIntosh (19 taxa, of which six taxa are shared; 1996). Both the Antero and Pitch-Pinnacle floras are small and have only a few temperate dicots in common with nearby Florissant. Their pollen floras are both dominated by similar gymnosperm pollen (our data, unpublished). Because of the clear similarity in composition, we suggest that Gregory and McIntosh's (1996) MAT value for Pitch-Pinnacle (12.7°C) be provisionally accepted for the Antero Flora. These are small floras, suggesting a major change after the Florissant interval. Meyer et al. (2012) suggest that summers were dry.

Creede Formation. The Creede flora of Colorado (26.5 Ma) is a highly limited, sparse flora, generally dominated by gymnosperms. Evidence from megafossils, the new pollen data (ca. 14 megafossil species and 21 pollen genera, including *Abies* cf. *bracteata* and *Picea sonomensis* Axelrod [*P.* cf. *breweriana*]), and the full list of identified dicots needs to be considered (see Table 4).

The first comprehensive flora of the Late Oligocene Creede Formation was published by Axelrod (1987), who described 73 species and ca. 40 genera of vascular plants. Later work by Wolfe and Schorn (1989, 1990) reviewed the previous flora by Axelrod and reduced the number of taxa to only 31 species and 21 genera. Using nearest living relatives method, Axelrod considered the flora to represent a relatively warm mean annual temperature (11.5°C). Using Climate Leaf Analysis Multivariate Program (CLAMP), a leaf morphology method for analyzing climate utilizing a suite of ca. 30 dicotyledonous leaf characteristics, Wolfe and Schorn declared the mean annual temperature to have been < 2.5°C, and later, 4°C. We have reinstated several of Axelrod's (1987) dicot genera, because we found them in the Creede pollen record. Based on pollen we have added two new conifers, three new families, and several new plant genera to the Creede flora (unpublished; a few are listed in Tables 3 and 4). These are a basis for reevaluating Wolfe and Schorn's proposed MAT for the Creede flora.

The associated dicot flora may broadcast the conditions of the Creede setting. We have found several of the dicot genera identified by Axelrod (1987) in the pollen record at Creede, which re-expands the flora from Wolfe and Schorn (1990). The pollen record seems to represent a wider signal of regional diversity in the Oligocene than does the megafossil foliage list alone; Table 4 shows the identifications by various authors at the Creede crater. It is probably significant that a few of the identified dicot genera have representative species growing today in areas of low summer precipitation in Monterrey County, California, and/or in nearby west slope California areas.

The vegetation at Creede suggested by the abundant Pinaceae pollen (e.g., Fig. 11, Appendix 3) generally corroborates the conclusion from megafossils that the Creede vegetation was a coniferous montane forest, with a prominence of *Pinus* + *Abies* pollen (7%–25%), *Keteleeria*-type (3.5%–20%), and with some *Picea* (3%–9%). *Podocarpus* pollen is also regularly present. The abundance of Abietineae and the presence of *Pinus crossii* (*Pinus* cf. *aristata*) megafossils suggest that the forest was an upper montane setting. However, the other aspects of the megaflora, such as rosaceous shrubs *Prunus* L. and *Cercis* L., and *Catalpa* Scop. (a de-

TABLE 4. List of dicot genera identified as megafossils by various authors from the Creede Formation (Late Oligocene), Colorado. Twelve of the 20 genera are also identified in the Creede pollen record; these are marked with an asterisk (*).

Dicot genera of the Creede Formation	Det. by Knowlton (1923)	Det. by Axelrod (1987)	Det. by Wolfe and Schorn (1989, 1990)	Det. by pollen, this report
Acer L.*	—	×	—	×
Alnus Mill.*	×	×	—	×
Berberis L.	—	×	×	×
Betula L.*	—	×	—	×
Cercis L.	—	×	×	—
Cercocarpus Kunth.	—	×	×	—
Fraxinus L.*	—	×	—	×
Jamesia Rafin.	—	×	×	—
Juglans L. (reworked)	—	—	—	x?
Myrica L.*	×	—	—	×
Nuphar Sibth. & Sm.	—	×	—	—
Populus L.*	×	×	×	×
Prunus L.*	—	×	×	x?
Quercus L.*	—	×	—	×
Ribes L.*	×	×	×	×
Salix L.*	×	×	×	×
Shepherdia Nutt.*	—	×	—	×
Sorbus L.	—	×	×	—
Ulmaceae L.*	×	—	—	×
Catalpa Scop.	—	—	×	—

ciduous tree), suggest that a middle montane setting might be the case.

Taken together, the Colorado pollen and megafossil data both record a significant drop in the role and diversity of hardwood genera (arboreal dicot pollen or "Dicot AP" in Fig. 11). Deciduous hardwoods need at least 800 mm of annual precipitation to function in summertime, while the conifers can reproduce with far less (Waring & Franklin, 1979; Thompson et al., 1999b). The rapid change in dominant taxa from deciduous hardwood to conifer supports a conclusion of precipitous cooling and drying after the end of the Eocene.

Based on our reevaluation of Wolfe and Schorn's (1989) or Wolfe's (1993) later assessment at Creede, the estimated 9°C MAT at Creede, lowered from 15°C at Florissant, is about a 6°C drop in MAT during the Oligocene (Table 2), which is enormous. The data suggest that based on the Antero pollen and the Pitch-Pinnacle flora (Gregory & McIntosh, 1996), cooling began ca. 500,000 years after the Florissant interval and continued through Creede time at 26 Ma. It seems to reflect the global cooling documented by Zachos at 33 Ma until ca. 26 Ma as outlined in Figure 13A (Zachos et al., 2001). In Europe, a parallel drop in MAT of ca. 5°C is demonstrated by the central European floras from Early Rupellian time to mid-Chattian time (Mosbrugger et al., 2005). West Coast floras also suffered a similar lowering of MAT and drying conditions (Retallack et al., 2004). In Alaska, Ridgeway et al. (1995) report a sudden drop in diversity of hardwood trees and

increase in conifers in the pollen counts across the Eocene–Oligocene transition.

At Creede, Axelrod (1987) thought that precipitation occurred chiefly in the warm season, but Wolfe and Schorn (1989) disagreed, since the flora suggests that the Creede climate had dry summers. Our data on the paucity of dicot hardwoods and the abundance of desert-adapted taxa, such as *Ephedra* (3 spp.), *Sarcobatus*, and *Artemisia*, reinforce Wolfe and Schorn's conclusion that dry summer conditions existed at Creede. It seems likely that the shortage of growing-season rainfall as well as the cooling contributed to the demise of *Abies* cf. *bracteata* populations in Colorado; Axelrod (1988) also argued that as summers became drier, germinating seedlings failed to become established (in the mixed conifer zone).

BIOGEOGRAPHY—THE RANGE DISPLACEMENT OF THE *ABIES BRACTEATA* LINEAGE

It is of special interest that section *Bracteata* megafossils were well represented in the central Rocky Mountains during the Oligocene, and that by Early Oligocene *Abies* cf. *bracteata* forms had spread to the Pacific Northwest (Rujada flora; Lakhanpal, 1958).

In younger Miocene sediments to the west, the habitats and forest types where section *Bracteata* continued were in mixed hardwood forest: in Nevada (Purple Mountain, Middlegate, Upper Cedarville), in Oregon (Mascall, Stinking Water) and in Idaho (Clarkia). These floras record a warmer climate of around 11°C–12°C in mean annual temperature (Fig. 13B), and the vegetation suggests a summer-moist climate. The vegetation

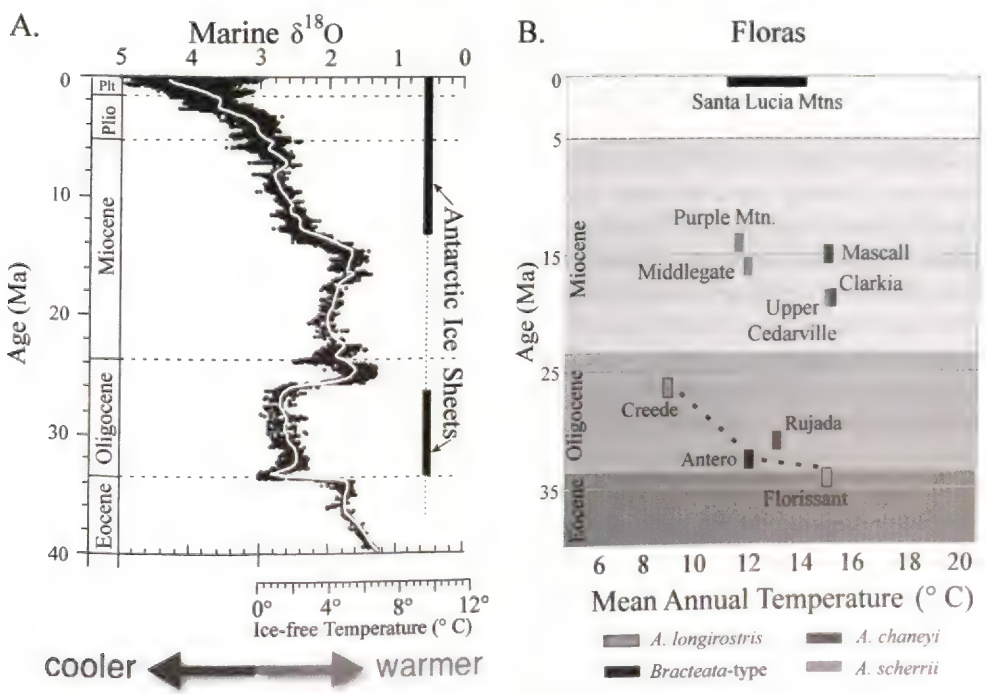


FIGURE 13. —A. The Zachos et al. (2001) marine curve, indicating global temperature change based on $\delta^{18}O$ data. —B. Estimated MAT (°C) at *Abies* sect. *Bracteata*-type fossil localities arranged chronologically. The depressed temperature following the Florissant interval suggests an abrupt cooling during the Oligocene.

of Mascall was indeed a rich hardwood sclerophyllous forest not so different from the associations that *Abies bracteata* has today (Chaney & Axelrod, 1959; Whittaker, 1961). The geographic position of these sites (Fig. 1) establishes that section *Bracteata* once spanned the western states, and that its range in the mid continent shrank as it disappeared from the Rocky Mountain area sometime after the Oligocene. By Late Miocene time the lineage was apparently absent in Rocky Mountain floras of Colorado, Wyoming, and Idaho (Trapper Creek [Axelrod, 1964]; Troublesome [Leopold, 1969]; Teewinot [Barnosky, 1984]; Glenns Ferry [Leopold & Wright, 1985]; Split Rock [Leopold & Denton, 1987]). However, across the Pacific Northwest and Nevada, megafossils of section *Bracteata* were fairly common in the Middle and Late Miocene. Axelrod (1985) suggested that these westerly Miocene floras had precipitation adequate to support sclerophyllous hardwood vegetation, and a mean annual temperature several degrees warmer than that of the Late Oligocene in Colorado. Ultimately *Abies* sect. *Bracteata* became endemic in the California coastal mountains area, probably as a result of the global Pleistocene climate changes, with major swings of cold climate and precipitation. The Oligocene temperature pattern we estimate was broadly similar to that recorded in the global marine curve in $\delta^{18}O$ (Fig. 13A; Zachos et al., 2001).

Abies sect. *Bracteata* was not the only conifer to show this western displacement. *Sequoia affinis* Lesquereux (cf. *Sequoia sempervirens*, coastal redwood) and *Torreya bonseri* (Knowlton) LaMotte (cf. *Torreya californica*, California nutmeg) also showed a widespread occurrence in the Rocky Mountains during the mid-Cenozoic (Chaney, 1948; MacGinitie, 1953) but lost ground in the later Tertiary. Other examples include *Sequoiadendron* (Miocene of California and Nevada) and *Picea sonomensis* Axelrod (*Picea* cf. *breweriana)* known from the Creede and the Miocene of Idaho. *Pinus balfouroides* Axelrod (*Pinus* cf. *balfouriana*), *Lithocarpus*, and *Arbutus* L. grew together in Nevada at the Purple Mountain and Middlegate floras in the Miocene, but endured range displacement later to become endemic along the West Coast. Whittaker described this general biogeographical pattern in a monumental paper in 1961.

In summary, *Abies bracteata* is one of many plants with a former history in the western United States that had once thrived in relatively warm, equable climates and moderate precipitation conditions. These taxa appear to show a response to changes in climate. Mean annual temperature at the end of the Eocene dropped at least 6°C. For 7 million years the climate became cooler in the Oligocene; this coincided with the opening of the Drake Passage (Graham, 2011) and the period of extreme explosive volcanism in Colorado, including the colossal Fish Canyon Tuff event of La Garita caldera (Lipman et al., 1996). Temperatures increased at the end of the Oligocene (Zachos et al., 2001), reaching a peak at mid-Miocene as shown at Clarkia (Kvaček & Rember, 2000). Because there were few physical barriers to the moist westerlies during the Oligocene (Durden, 1966; Axelrod, 1976), rainfall was probably higher than now. The major factor that eliminated several plant species from the Rocky Mountain area during the Oligocene (including *Abies* sect. *Bracteata*) may have been the cooling, along with conditions of summer drought.

How do these biogeographic changes relate to continental uplift in the mid continent? Data from recent studies documenting the timing of uplift in the Rocky Mountain region suggest that an initial gradual uplift of the Colorado Plateau began at 25 Ma, and that a more severe and rapid uplift occurred beginning at 5 Ma (Sahagian et al., 2002), long after the Creede flora time. According to data in Table 2, these Tertiary floras were all deposited at elevations lower than present, except perhaps Middlegate and Rujada.

While there is considerable evidence from marine patterns of $\delta^{18}O$ that the Oligocene cooling in Colorado was part of a global cooling (Zachos et al., 2001), topographic change due to Late Neo-

gene uplift in Colorado would have also impacted its climate and vegetation.

Although there are no records so far of post-Miocene fossil occurrences of the *Abies bracteata* lineage, it is easy to imagine that the strong climatic shifts of the Quaternary may have had further deleterious effects to limit the distribution of the group.

CONCLUSIONS

In our study of pollen morphology of *Abies*, we found that the pollen of this group have specific features that allow identification of the section *Bracteata*-type as a minor element in the Rocky Mountain floras. Though the relative abundance of section *Bracteata* pollen morphotype is low, nevertheless the identified characteristics of section *Bracteata*-type pollen are distinctive enough that the morphotype can be used to signal its presence in fossil floras. The combination in *Abies* of low Eq/P pollen cell ratio, thick cappus, and relatively large size is only found in section *Bracteata*-type pollen, according to our survey.

Abies sect. *Bracteata* was once widespread in the western United States, first appearing in Colorado (Florissant, Late Eocene) and in Oregon (Rujada, Oligocene). In the Rocky Mountains, section *Bracteata* was initially associated with the subtropical to warm temperate mesophytic forest at Florissant, where it grew with *Sequoia* and *Torreya*. Later it became associated with a dominantly coniferous cool and somewhat dry temperate forest at the Antero (33 Ma) and Creede (26.5 Ma) formations in Colorado. The abundance of *Abies* sect. *Bracteata* megafossils is typically low, except at two stations at Creede. The lineage may have been a minor element in western floras, but was a consistent marker fossil for Oligocene sediments in Colorado.

After the Oligocene, the geographic range of *Abies* sect. *Bracteata* shifted westward; megafossils were found in the Miocene of Nevada and the Pacific Northwest, where they were associated with *Sequoiadendron* and species ancestral to *Picea breweriana*, *Pinus balfouriana*, and others, especially dicot sclerophylls. This suggests low summer precipitation with occasional summer showers, much like conditions today in the Klamath Mountains (Whittaker, 1961; Axelrod, 1995). In the mid-Miocene, *Abies* sect. *Bracteata* was apparently absent in the Colorado Rocky Mountain area. The change demonstrates an initial shrinkage of its geographic range, probably induced by cooling and reduction of precipitation. A second shrinkage of range occurred after the Miocene, when fossil floras in the western states demonstrated a lowering of summer rainfall and the onset of a summer-dry climate.

The cooling and drying of the Oligocene began immediately after the Florissant flora and continued for the next 7 million years. This climatic shift follows the opening of the Drake Passage and the interval of explosive Colorado volcanism. Climatic warming followed, peaking in the mid-Miocene. We conjecture that the range displacement for *Abies* sect. *Bracteata* from Colorado at the end of the Oligocene probably resulted from cooling and from lower summer precipitation, as was generally suggested by Wolfe and Schorn (1990). From these data, it appears that *Abies* sect. *Bracteata* endured the greatest rapid climatic deterioration of the Tertiary record: a lowering of MAT by around 6°C (from 15°C at Florissant to 12°C at Antero and 9°C at Creede; this report). This shift occurred in southern Colorado, but was also felt to some degree in the Pacific Northwest (Retallack et al., 2004; Leopold et al., 2008), Alaska (Ridgeway et al., 1995), and Europe (Mosbrugger et al., 2005).

These changes were probably exacerbated by the shift to a summer-dry climate in the Late Miocene of Colorado, and may have been reinforced later by the beginning of major uplift of the Colorado Plateau after the latest Miocene (Sahagian et al., 2002), as well as the lifting of the Cascades (Cheney & Hayman, 2007).

Abies sect. *Bracteata* was one of several conifer lineages once widespread in the Rocky Mountains that became dispersed westward during the Oligocene, only to be lost from the Pacific Northwest flora after the end of the Miocene. The pattern follows the general pattern of range displacement suggested by Whittaker (1961) for the Pacific Coast states.

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LITERATURE CITED

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APPENDIX 1. Reference pollen slides used in this report. U.S.G.S. "P" numbers refer to modern pollen preparations in the U.S. Geological Survey Denver lab. Jane Gray preparations of modern pollen are marked with the preparation date and the initials "JG." Modern pollen preparations at the University of Washington (UW) pollen lab are marked with an "S" number (for Seattle). Estella Leopold preparations of modern pollen are marked with the initials "EBL." Pan American Oil Company preparations of modern pollen are marked with the abbreviation "PanAm." Preparations from the Yale herbarium (YU) carry only Leopold's student numbers. Herbarium codes can be found at <http://sweetgum.nybg.org/ih/>.

Section (per Liu, 1971)	*Abies* species (total no. of grains studied)	Source	Herbarium sheet no.	Collector, date, no.	Locality in general terms
Abies	*A. alba* Mill. (3)	Reille, 1992	no info	no info	no info
	A. cephalonica Loudon (10)	Reille, 1992	no info	no info	Greece
		UW S1200	no info	E. Leopold 1980	rd. from Arachova to Orhomenos, Greece
	A. cilicica (Antoine & Kotschy) Carrière (3)	Reille, 1992	no info	no info	no info
	A. nebrodensis (Lojac.) Mattei (2)	Reille, 1992	no info	no info	no info
	A. nordmanniana (Steven) Spach (2)	Reille, 1992	no info	no info	no info
	A. bornmuelleriana Mattf. (1); syn. *A. nordmanniana* var. *bornmuelleriana* (Mattf.) Silba by Farjon and Rushforth, 1989	Reille, 1992	no info	no info	no info
Amabilis	*A. amabilis* Douglas ex J. Forbes (17)	JG 11/5/67	ORE	Andrews 1936, #544	Lake Co., Oregon, U.S.A.
		U.S.G.S. P1066	USE 336994	Allen 1897, #313	Washington State, U.S.A.
		U.S.G.S. P3446	no info	J. F. Franklin 1964	Skamania Co., Washington, U.S.A.
		U.S.G.S. P3447	no info	J. F. Franklin 1965	Linn Co., Oregon, U.S.A.
		UW S205	no info	R. Nickmann 1978	Seattle, Washington, U.S.A.
	A. mariesii Mast. (14)	JG 6/28/61	no info	T. Jimbo 1951	Mt. Hakkoda, Honshu, Japan
Balsamea	*A. balsamea* (L.) Mill. (14)	EBL-99	YU	Eaton 1894	Mt. Washington, New Hampshire, U.S.A.
		JG 2/15/57	TEX	Fernald 1900	no info
		U.S.G.S. P1068	US 940822	J. D. Smith 1888, #899	New Brunswick, Canada
	A. fraseri (Pursh) Poir. (15)	Dan Livingstone slide	DUKE 89674	McQuiskin	Mt. Mitchell, North Carolina, U.S.A.
	A. kawakamii (Hayata) T. Itô (1)	Huang, 1972	no info	no info	no info
	A. lasiocarpa (Hook.) Nutt. (11)	EBL #11	YU	collected 1883	Washington State, U.S.A.
		JG 11/23/70	OSC 87874	Seward 1954, #6715	near Santiam Pass, Oregon, U.S.A.
		JG B2 2/2/66	ORE	Henderson 1934, #16412	Lane Co., Oregon, U.S.A.
		U.S.G.S. P3443	no info	J. F. Franklin 1965	Linn Co., Oregon, U.S.A.
		U.S.G.S. P3444	no info	J. F. Franklin 1965	Linn Co., Oregon, U.S.A.

		U.S.G.S. P634	US 1765547	Preston 1937, #8335	Colorado, U.S.A.
		UW S218	no info	U.S.F.S. L Lot U	Santiam Pass, Linn Co., Oregon, U.S.A.
		UW S233	no info	U.S.F.S. LA Lot C	Coconino Co., Arizona, U.S.A.
	A. nephrolepis (Trautv. ex Maxim.) Maxim. (1)	Erdtman, 1957	no info	no info	no info
	A. sibirica Ledeb. (1)	Erdtman, 1943	no info	no info	no info
	A. vertchii Lindl. (14)	JG 01/1962	no info	J. Nakamura	Kochi Prefect, Shikoku, Japan
Bracteata	*A. bracteata* D. Don (Port.) (18)	JG 12/11/55	UC 223992	Plaskett 1898, #109	Monterey Co., California, U.S.A.
		UW slide S225	no info	U.S.F.S. 1975, Lot P	Tilden Park, California, U.S.A.
		UW slide S226	no info	U.S.F.S. 1975, Lot Q	Tilden Park, California, U.S.A.
		U.S.G.S. P2413	UC 139982	Plaskett 1898, #109	Santa Lucia Mtns., California, U.S.A.
		U.S.G.S. P633	US 341416	Plaskett, #109	California, U.S.A.
Grandis	*A. grandis* (Douglas ex D. Don) Lindl. (21)	U.S.G.S. P3442	no info	J. F. Franklin 1965	Linn Co., Oregon, U.S.A.
		U.S.G.S. P3445	no info	J. F. Franklin 1964	Benton Co., Oregon, U.S.A.
		UW S231	no info	U.S.F.S. 1971 G Lot V	Irish Beach, California, U.S.A.
		UW S236	no info	U.S.F.S. 1971 Lot AH	Corvallis, Oregon, U.S.A.
		UW S237	no info	U.S.F.S. 1971 Lot AL	Corvallis, Oregon, U.S.A.
		UW S241	no info	U.S.F.S. 1971 Lot AH	Corvallis, Oregon, U.S.A.
	A. concolor Lindl. & Gordon (19)	slide 7/23/53	YU	"93"	Arizona, U.S.A.
		U.S.G.S. P1069	US 247207	M. E. Jones 1878	Colorado, U.S.A.
		UW S215	no info	U.S.F.S. 1971 C ELD-4-2	El Dorado Co., California, U.S.A.
		UW S228	no info	U.S.F.S. 1971 Lot AM	Corvallis, Oregon, U.S.A.
Mam.	*A. firma* Siebold & Zucc. (10)	JG 12/1961	no info	J. Nakamura	Kochi Prefect, Shikoku, Japan
	A. chensiensis Tiegh. (syn. *A. ernestii* Rehder) (1)	Wang et al., 1995	no info	no info	no info
Nobilis	*A. procera* Rehder (17)	PanAm M598	no info	ASGJ #398	Corvallis, Oregon, U.S.A.
		U.S.G.S. P3448	no info	J. F. Franklin 1965	Linn Co., Oregon, U.S.A.
		U.S.G.S. P3449	no info	J. F. Franklin 1965	Benton Co., Oregon, U.S.A.
		U.S.G.S. P3450	no info	J. F. Franklin 1965	Larch Mt., Oregon, U.S.A.
		UW S243	no info	U.S.F.S. 1968 Lot A H	Iron Mt., Linn Co., Oregon, U.S.A.
		UW S245	no info	U.S.F.S. 1968 Lot A F	Iron Mt., Linn Co., Oregon, U.S.A.
		UW S246	no info	U.S.F.S. 1968 Lot A I	Linn Co., Oregon, U.S.A.

(*continued*)

Section (per Liu, 1971)	*Abies* species (total no. of grains studied)	Source	Herbarium sheet no.	Collector, date, no.	Locality in general terms
	A. magnifica A. Murray bis (14)	JG 11/20/55	UC 55655	Chandler #1684	Siskiyou Co., Oregon, U.S.A.
		JG 3/1/68	OSC 25713	Kildale 1930, #10178	Trinity Co., California, U.S.A.
		JG 3/23/56	UC 747688	Robbins 1943, #1213	El Dorado Co., California, U.S.A.
		PanAm M600	no info	ASGJ #25710	Ashland Butte, Oregon, U.S.A.
Piceaster	*A. pinsapo* Boiss. (3)	Arista & Talavera, 1994: 228	no info	no info	no info
	A. pinsapo var. *marocana* (Trab.) Ceballos & Martín Bol.	Reille, 1992	no info	no info	no info
	A. numidica de Lannoy ex Carrière (1)	Reille, 1992	no info	no info	no info
Pseudopicea	*A. delavayi* Franch. (1)	Wang et al., 1995	no info	no info	no info
	A. georgei Orr (1); called *A. forrestii* Coltm-Rog. var. *georgei* (Orr) Farjon by Farjon and Rushforth, 1989	Wang et al., 1995	no info	no info	no info
	A. squamata Mast. (1)	Wang et al., 1995	no info	no info	no info

APPENDIX 2. Measurements of modern *Abies* pollen from reference slides. For slide numbers and image sources see Appendix 1.

Section (per Liu, 1971)	Species (total no. of grains studied)	Total length of bladder (µm)	Equator (µm)	Pole (µm)	Bladder pole (µm)	Cappus (µm)	Cappus shoulder	Ratio Equator to Pole (Eq/P)	SD Eq/P	SD Shoulder
Abies	*A. alba* Mill. (3)	119.33	80.25	59.25	39.30	4.35	8.10	1.37	—	—
	A. cephalonica Loudon (10)	157.37	115.84	82.51	52.62	7.73	11.15	1.41	0.19	1.29
	A. cilicica (Antoine & Kotschy) Carrière (3)	179.40	132.00	100.33	47.47	6.15	7.95	1.32	—	—
	A. nebrodensis (Lojac.) Mattei (2)	174.15	139.75	83.55	39.15	5.95	4.40	1.67	—	—
	A. nordmanniana (Steven) Spach (2)	211.06	155.56	98.76	57.20	4.21	8.42	1.58	—	—
	A. bornmuelleriana Mattf. (1); called *A. nordmanniana* var. *bornmuelleriana* (Mattf.) Silba by Farjon and Rushforth, 1989	185.85	129.60	86.40	58.50	11.25	12.60	1.50	—	—
Amabilis	*A. amabilis* Douglas ex J. Forbes (17)	156.55	122.61	84.16	36.40	3.99	7.22	1.47	0.19	1.81
	A. *mariesii* Mast. (14)	**192.94**	**153.27**	**96.83**	**59.85**	**4.04**	**7.98**	**1.59**	**0.10**	**0.77**
Balsamea	*A. balsamea* (L.) Mill. (14)	154.89	119.73	87.52	48.26	5.24	5.98	1.41	0.22	2.46
	A. *fraseri* (Pursh) Poir. (15)	**159.69**	**120.97**	**94.34**	**30.40**	**4.35**	**5.85**	**1.29**	**0.13**	**2.35**
	A. kawakamii (Hayata) T. Itô (1)	128.70	94.50	70.20	30.10	5.60	5.60	1.35	—	—
	A. *lasiocarpa* (Hook.) Nutt. (11)	**135.56**	**104.91**	**75.90**	**35.49**	**4.50**	**6.06**	**1.39**	**0.11**	**1.92**
	A. nephrolepis (Trautv. ex Maxim.) Maxim. (1)	157.70	108.90	82.60	45.00	3.30	5.10	1.32	—	—
	A. *sibirica* Ledeb. (1)	**149.00**	**119.00**	**82.00**	**66.86**	**4.80**	**5.70**	**1.45**	—	—
	A. veitchii Lindl. (14)	83.73	62.66	43.68	23.95	3.39	5.01	1.45	0.14	0.96
Bracteata	*A. bracteata* D. Don (Poit.) (18)	169.07	126.47	105.09	47.72	7.06	9.72	1.21	0.07	1.15
Grandis	*A. grandis* (Douglas ex D. Don) Lindl. type (21)	156.90	125.86	94.15	33.71	5.20	8.18	1.35	0.14	1.66
	A. *concolor* Lindl. & Gordon (19)	**159.96**	**127.96**	**96.71**	**46.46**	**4.17**	**7.66**	**1.34**	**0.16**	**1.80**
Momi	*A. firma* Siebold & Zucc. (10)	121.70	101.56	67.26	30.05	5.33	6.49	1.52	0.12	0.94
Nobilis	**A. *procera* Rehder (17)**	**173.86**	**127.36**	**95.99**	**46.45**	**4.67**	**7.34**	**1.34**	**0.12**	**1.23**
	A. magnifica A. Murray bis (14)	188.96	145.17	105.93	60.28	4.98	7.58	1.36	0.13	1.70
Piceaster	*A. pinsapo* Boiss., *A. pinsapo* var. *marocana* (Trab.) Ceballos & Martín Bol. (3)	136.89	102.19	79.86	35.79	3.54	6.79	1.29	—	—
	A. numidica de Lannoy ex Carrière (1)	206.46	142.02	116.77	54.70	4.47	5.52	1.22	—	—
Pseudopicea	*A. delavayi* Franch. (1)	183.80	158.00	112.80	42.80	6.80	6.40	1.50	—	—

APPENDIX 3. *Pollen/spore counts of Paleogene collections from central and southern Colorado. "D" numbers are U.S. Geological Survey paleobotany locality numbers. "R" numbers were obtained through the Colorado Museum at Boulder, courtesy of Dena Smith. "AP dicots" indicates pollen from arboreal dicotyledons; "NAP dicots" indicates pollen from non-tree dicotyledons. "TCT" = pollen from "Taxodiaceae"/Cupressaceae/Taxaceae.*

			Florissant			Antero			Creede		
Groups		Taxa	D1083 3/15/12 (%)	D3496 3/15/12 (%)	D1496 Fish Beds Recount 10/1/12 (%)	R2063-3/ OTC (1) 3/15/12 (%)	R2910-1/ OTC "101" 8/24/12 (%)	D1181-18 Recount 8/15/12 (%)	D4294A (2) Five Mi Bridge 10/15/12 (%)	D4293G (2) 8/20/12 (%)	R2912-3 "1" 7/11/12 (%)
Gymnosperms	Pinaceae	small pine				2.5	6.1	13.1	3.8	1.3	6.7
		Pinus L.	2.7	11.8	22.9	31.0	24.8	28.4	54.3	30.2	31.6
		Picea A. Dietr.	5.7	3.2	4.2	34.7	7.5	9.1	3.2	8.6	8.3
		Abies Mill.	0.6	4.2	1.4	3.1	2.3	7.3	4.1	5.3	25.6
		A. concolor Lindl. & Gordon type						2.4			
		A. bracteata (D. Don) Poit. type	0.9	1.0	0.3	0.3	0.6	0.3	1.8	1.5	0.6
		Keteleeria Carrière type				5.2	8.1	20.4	3.5	6.6	4.8
		Cathaya Chun & Kuang type					1.2				0.3
		Larix Mill.	0.3		0.3	0.9	2.9	0.3			0.3
		Tsuga Carrière				2.1	0.3				0.3
		undet. Pinaceae		0.3	0.2	0.3	3.2	4.6	11.4	4.0	
	Other	"TCT"	65.0	40.9	7.0		3.7	2.1	0.3	2.4	3.2
		Podocarpus L'Hér. ex Pers. type		2.2	0.5	0.9	0.3	0.6	0.6	0.7	1.6
		Ephedra L.		1.3	0.5	0.9	2.6	2.4	1.8	6.2	2.2
		Total gymnosperms	75.2	64.9	37.3	81.9	63.4	91.4	85.0	66.7	85.6

AP dicots	*Acer* L.			0.3		0.6			
	Alnus Mill. sp.				0.3			0.3	
	Betulaceae	0.3		0.7	3.1				
	Carya Nutt.	1.5	0.6	5.6		3.2			
	Castanea Mill. type							0.2	
	Celtis L.			0.2		0.6			
	Eucommia Oliv.		0.3	0.2					
	Fremontia Torr.		0.3						
	Other AP dicots			39.4				0.6	0.2
	Engelhardia Lesch. ex Blume		0.3						
	cf *Fagus* L.								0.3?
	Itea L.		0.3						
	Juglandaceae		13.1			6.1	0.3		
	Juglans L.	3.3		2.8	1.8	0.6		0.6	0.2
	Ostrya Scop.	0.3			0.3	1.2			0.2
	Pterocarya Kunth	0.6		1.4	0.3	0.9		0.3	
	Quercus L. type	0.6		0.5			0.6		0.7
	Ulmus L./Ulmaceae	1.2	4.8	1.2		5.2			
	Total AP dicots	7.9	19.8	52.4	11.0	18.2	0.9	1.8	1.5	0.3
NAP dicots	Amaranthaceae			1.2	0.3					0.3
	Arceuthobium M. Bieb.				0.3				
	Artemisia L.							0.3	0.7	
	Other NAP dicots	5.4	0.3	5.6	4.0	12.1	2.8	6.2	11.0	2.2
	Ribes L.	0.3								
	Sarcobatus Nees	0.6		2.3	0.3	5.2	4.3	7.1	20.3	9.9
	Shepherdia Nutt.						0.3			
	Total NAP dicots	6.3	0.3	9.1	4.9	17.3	7.3	13.2	31.3	12.5
	Total monocots	1.5		0.7	0.9	0.9			0.2	0.3

(*continued*)

		Florissant			Antero			Creede		
Groups	Taxa	D1083 3/15/12 (%)	D3496 3/15/12 (%)	D1496 Fish Beds Recount 10/1/12 (%)	R2063-3/ OTC (1) 3/15/12 (%)	R2910-1/ OTC "101" 8/24/12 (%)	D1181-18 Recount 8/15/12 (%)	D4294A (2) Five Mi Bridge 10/15/12 (%)	D4293G (2) 8/20/12 (%)	R2912-3 "1" 7/11/12 (%)
Other	Colpate	4.8	8.6							1.0
	Porate	2.7	5.1							0.3
	Trilete	1.2	1.3	0.5	1.2	0.3		0.3		
	Trilete: *Selaginella* P. Beauv.	0.3					0.3		0.3	
	Total other	9.1	15.0	0.5	1.2	0.3	0.3	0.3	0.2	1.3
	Total (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	Total count (no. of pollen grains)	331	313	573	326	347	327	341	454	313

SELECTED SUMMARIES	Florissant			Antero			Creede		
Total Pinaceae pollen (%)	10.3	20.4	29.3	80.1	56.8	86.2	82.4	57.5	78.6
Total hardwood trees (arboreal pollen) (%)	7.9	19.8	52.4	11.0	18.2	0.9	1.8	1.5	0.3
Total non-tree pollen (%)	6.3	0.3	9.1	4.9	17.3	7.3	13.2	31.3	12.5

CHAPTER 10

THE INFLUENCE OF REGIONAL HISTORY AND ECOLOGICAL AFFINITY IN THE ANGIOSPERM COMPOSITION OF MEXICAN LOWLAND TROPICAL RAINFORESTS

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ABSTRACT

In contrast to a substantial part of the Neotropical realm, the northern Neotropical region, which is occupied today by the territories of Mexico and northern Central America, geologically belongs to Laurasia. Between the Early Cretaceous, when angiosperms started to diversify, and the Early Eocene global thermal maximum, when megathermal floras extended to high latitudes in the Northern Hemisphere, what is now Mexico was physically and biotically continuous with the rest of Laurasia. Its Laurasian history and biotic connectivity are thus expected to provide a signature in the composition of present-day Mexican megathermal floras, particularly in lowland tropical rainforests (LTRFs). Ecological affinity, through phylogenetic niche conservatism, is also a powerful determinant of biotic composition. If phylogenetic niche conservatism is prevalent, it would be expected that Mexican LTRFs are preferentially occupied by members of lineages adapted to the physical conditions of LTRFs. In this study, we evaluate the relative role of regional history and ecological affinity in the angiosperm composition of Mexican LTRFs. First, by using indices of floristic similarity, we investigated if Mexican LTRFs are more similar to floras of the same geographical region but of different biomes, or to LTRF floras from different geographical locations. We compared the LTRFs of Mexico (LTRFs-M) with the floras of four different biomes found in Mexico, and of 13 LTRFs from Central America, South America, and Africa. The LTRFs-M were found to be most similar to humid montane forests of Mexico, with which they share a geological history and several important ecological parameters. Subsequently, by implementing an index based on the relative abundance of a given family in the LTRFs-M and a comparison flora, we identified angiosperm families that characterize the LTRFs-M with respect to other floras. Families whose presence in the LTRFs-M is possibly a consequence of regional influence are Asteraceae and Fagaceae, whereas families that possibly are present mostly due to ecological affinity following dispersal include Sapotaceae, Rubiaceae, Melastomataceae, and Moraceae. Finally, we attempted to determine if families that diversified before the onset of the Late Eocene cooling trend in LTRF floras are preferentially represented in LTRFs, by considering the relative

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preponderance of "ancestral" or "derived" lineages in LTRF floras with respect to the global flora. Intermediate phylogenetic levels were found to be overrepresented in LTRFs. In summary, regional composition and ecological affinity were both found to be important factors determining the composition of Mexican LTRFs.

Key words: AltGower dissimilarity index, beta diversity, biodiversity, biotic interchange, global thermal maximum, Laurasia, Neotropics, phylogenetic niche conservatism, phylogeny, plant diversity, tectonics.

The differential distribution of biodiversity around the globe is well recognized, but evolutionary causes underlying this pattern are not fully understood. The Neotropical realm (Udvardy, 1975) contains a vast amount of plant diversity (e.g., Prance, 1977; Gentry, 1982; Graham, 2010) including different biomes, substantial morphological and functional diversity, and high species richness. This diversity is the result, among other factors, of complex interactions between two geological regions that have been historically independent except in the recent past. Although the South American Neotropical region is geologically derived from western Gondwana, the northern Neotropical region, which is occupied today by the territory of Mexico and parts of Central America, tectonically corresponds to southwestern Laurasia. Except for the Baja California peninsula and possibly the Sierra Madre del Sur, which were apparently offshore island arcs that became accreted to the mainland at different times (Graham, 2010), the rest of the territory of Mexico constitutes a geologic unit with the rest of Laurasia, corresponding to the southwestern end of that landmass (Scotese, 2002). During most of the Cretaceous, southwestern Laurasia was almost entirely covered by an epicontinental sea, except for uplands along the axes of the incipient Sierra Madre Occidental and Sierra Madre Oriental. By the Early Tertiary, the interior lands had mostly emerged, and Mexico's modern landscape began to originate (Ferrusquía-Villafranca, 1993; Graham, 2010). Floristic connections with the rest of Laurasia are documented by fossil taxa shared between Tertiary localities in the U.S.A. and Mexico (e.g., Wendt, 1993; Magallón-Puebla & Cevallos-Ferriz, 1994a, 1994b).

In spite of prolonged and substantial efforts, a complete inventory of Mexican biodiversity has not yet been accomplished, due to the sheer species richness overlain on a physically complex area. Nevertheless, the currently available biodiversity information (e.g., CONABIO, 2008; Villaseñor & Ortiz, 2013) represents sufficient critical mass to start to investigate the processes underlying its species richness. This study is part of a wider research program to investigate how the Laurasian Neotropics, which include the Mesoamerican biodiversity hotspot (Myers et al., 2000), became species rich. We are particularly interested in the role of historical and evolutionary processes in the acquisition of plant diversity.

Explanations of Mexican species richness are usually based on extrinsic abiotic factors. Its territory accommodates a wide variety of physical, climatic, altitudinal, and edaphic conditions that are in close geographical proximity and therefore can accommodate many species with different ecological requirements. Two large mountain chains oriented in a north–south direction provide altitudinal and climatic variation and form biotic corridors along which temperate and tropical biotas come into contact. Coasts of two major oceans allow immigration from disparate geographical regions, including Europe, Africa, and the Asia-Pacific region. A complex tectonic history, including proximity to the contact zone between two major landmasses, allowed exchange between Laurasian and western Gondwanan biotas, while the migration and accretion of smaller

terrains allowed further biotic exchange, which is especially relevant at local levels. Due to its latitudinal position, Mexico is favored by global latitudinal biodiversity gradients (e.g., Wiens & Donoghue, 2004).

By themselves, these abiotic factors do not cause high species richness. They do so through their complex interactions and interplay with evolutionary factors, by influencing the rates of lineage diversification (i.e., net speciation) and migration that determine the richness of a region. The composition of a local biota is determined in part by the long-term geological and tectonic trajectory of a major geographical region (i.e., the regional history), but it is also affected by the capacity of organisms to survive in specific environmental conditions (i.e., their ecological affinity), which is influenced by phylogenetic niche conservatism (Donoghue, 2008; Crisp et al., 2009; see below). In this study, we investigate the role of regional history and of ecological affinity in determining the angiosperm (flowering plant) composition of lowland tropical rainforests (LTRFs) of Mexico (LTRFs-M; Fig. 1). We focus this study on angiosperms because they are the most diverse group among living plants, and they are also ecologically predominant, representing the structural and productivity basis of most present-day terrestrial ecosystems. The LTRFs of Mexico are inherently interesting because they represent the northernmost extension of this type of biome in the Neotropics. More specifically, because through most of their history they have developed in a region that is geologically distinct and geographically separated from that in which South American LTRFs develop, we expect that each has been influenced by different evolutionary trajectories.

The lowland tropical rainforest is a physiognomically distinctive biome found in particular environmental conditions and contains an extraordinarily high species richness (e.g., Whitmore, 1998). Characteristics of "archetypal" Neotropical rainforests are laid out by Burnham and Johnson (2004). They are typically multistratified systems dominated by large trees often exceeding 30 m in height, with emergents reaching over 45 m. Many trees have buttressed bases; leaves are evergreen, often large, and with characteristic drip tips. Lianas and epiphytes are abundant. Some of the most important families in this biome are Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Arecaceae. LTRFs develop in specific physical conditions, particularly regarding temperature (24°C mean annual temperature), precipitation (>2000 mm per year), humidity (>85%), and seasonality and altitudinal range (0–1000 m above sea level; Rzedowski, 1978). Globally, LTRFs occupy a disjunct intertropical band including the American continent, Africa, Asia, and Australia. LTRFs represent an excellent study system because they can be delimited on the basis of a distinct set of physical conditions that can be identified around the world, and because of the substantial amount of ecological and taxonomic studies to which they have been subjected.

Contrasting ideas have been set forth regarding the origin and affinities of Mexican LTRFs (Challenger, 1998; Challenger & Soberón, 2008). A. H. Gentry (1982) considered that tropical South American flora consists of Laurasian elements that migrated southward after the closure of the Panamanian isthmus and that are now ecologically prominent components of Andean floras, and of Gondwanan elements that are currently predominant in lowland floras. Gentry (1982) also proposed that Gondwanan taxa migrated from South America to tropical North America during two distinct periods: around the end-Cretaceous, via island hopping through intermittent connections in the proto-Antilles, leading to lineages that today occupy humid or arid environments and are strongly differentiated from their South American ancestors, and during the Pliocene and later times, as a consequence of the closure of the Panamanian isthmus, leading to taxa that are now

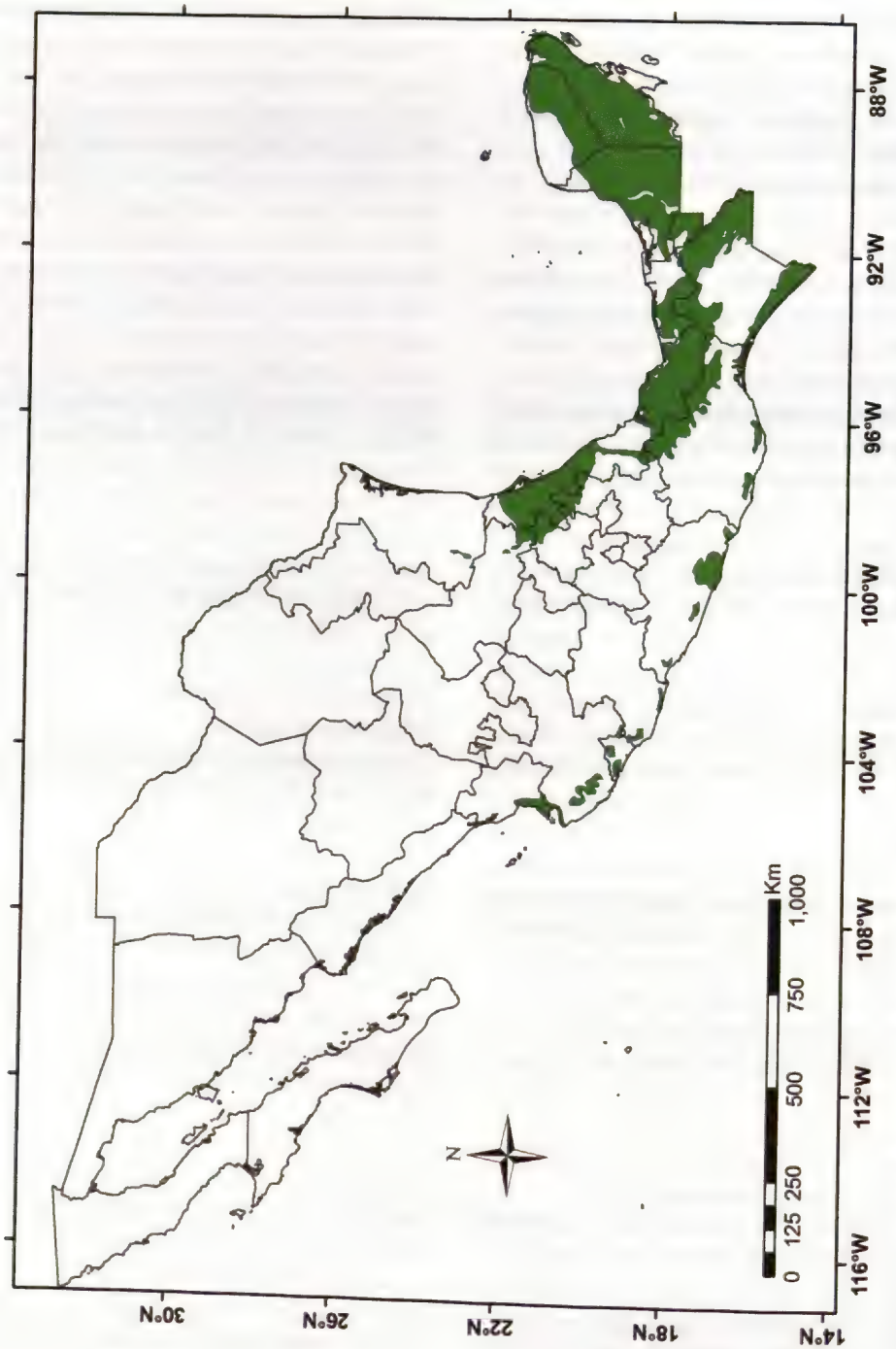

FIGURE 1. Geographical distribution of lowland tropical rainforests of Mexico (LTRFs-M).

canopy trees and lianas in lowland floras and are weakly differentiated from their South American ancestors.

In an evaluation of the canopy tree composition of Mexican Atlantic slope rainforests, T. Wendt (1993) concluded that an almost entirely South American composition of the modern Mexican rainforest flora is not supported and provided evidence for a greater relative importance of elements of Laurasian affinity. In particular, Wendt (1993) suggested that the modern rainforest composition results from complex processes involving changing climate and tectonic connections through the Late Cretaceous and Tertiary. He distinguished ancient elements derived from lineages of both Laurasian and Gondwanan origin that dispersed across Laurasian connections and that were present in North America during the Eocene, and elements derived from Neogene arrivals from South America. Taxa that have arrived at very different times through long-distance dispersal are also present (Wendt, 1993).

Regional history and ecological affinity are important determinants of local biotic composition. In particular, one part of the argument for the relevance of regional history derives from community ecology, which predicts that the biotic composition of a local community is a function of the regional pool (e.g., Cornell & Lawton, 1992; Ricklefs & Schluter, 1993). Between the Early Cretaceous, when angiosperm lineages started to diversify (Doyle, 2012), and the Early Eocene global thermal maximum, when megathermal floras extended to high latitudes in the Northern Hemisphere (Wolfe, 1985; Wolfe & Upchurch, 1987; Willis & McElwain, 2002), substantial biotic connections across Laurasia were available through long-term, but intermittent, links between North America (including the emerged parts of what is now Mexico) and Europe and Asia (Wolfe, 1975, 1985; Tiffney, 1985; Wing, 1987). The tectonic history associated with potential connections between southwestern Laurasia and South America is complex and not completely understood (e.g., Donnelly, 1985; Parrish, 1987; Ferrusquía-Villafranca, 1993; Wendt, 1993; Graham, 2010). Apparently, short-term stepping stone connections were available via a proto-Antillean arc during the Cretaceous, and via Antillean connections during the Tertiary, both before the establishment of the Central American land bridge formed by the closure of the Panamanian isthmus in the latest Neogene (latest Miocene to Pliocene; Savin & Douglas, 1985; Stehli & Webb, 1985; Wendt, 1993). The tectonic picture indicates that during the Late Cretaceous and Early Tertiary, when major components of the present-day flora diversified and became ecologically predominant, southwestern Laurasia had direct long-term biotic connections with the rest of Laurasia, whereas its possible connections with the South American landmass were intermittent and limited at best. We would therefore expect that because southwestern Laurasia apparently had limited connections with South America during most of the Cretaceous and Tertiary, and precluding the possibility of massive long-distance dispersal, the angiosperm composition of its present-day flora might be fundamentally Laurasian (Gentry, 1982; Wendt, 1993), suggesting a biotic differentiation of the Laurasian Neotropics from their South American counterpart.

The relevance of ecological affinity as a determinant of biotic composition is the consequence of phylogenetic niche conservatism—the observation that descendant lineages exhibit environmental tolerances and an ecological affinity similar to those of their ancestors (e.g., Harvey & Pagel, 1991; Ricklefs & Schluter, 1993; Ricklefs et al., 1999; Webb et al., 2002; Wiens, 2004; Wiens & Donoghue, 2004; Crisp et al., 2009; Wiens et al., 2010). We would therefore expect that a given biome is preferentially occupied by members of lineages that are adapted to the physical conditions of that biome, having arrived by dispersal through overland connections or even across oceans. M. J. Donoghue noted that when changing physical conditions result in new habitats,

these are preferentially occupied by migrants already adapted to the new conditions, rather than by organisms that originally inhabit the area but are not adapted to the new physical conditions; he succinctly summarized this concept by stating, "it's easier to move than to evolve" (Donoghue, 2008). If phylogenetic niche conservatism is dominant, we would expect ecological affinity to be a major determinant of the composition of the LTRFs of Mexico, and that their flora is more similar to that of LTRFs in other regions than to other biomes in the same geographical region.

The relative role of regional history and of ecological affinity in the angiosperm composition of Mexican LTRFs is here investigated by addressing the following questions: (1) is the angiosperm composition of Mexican LTRFs more similar to the regional flora, or to the flora of LTRFs from different geographical regions?; (2) which plant clades characterize Mexican LTRFs with respect to the regional flora?; (3) which plant clades characterize Mexican LTRFs with respect to the flora of LTRFs of different geographical regions?; and (4) are phylogenetically "ancestral" or "derived" lineages represented preferentially in Mexican LTRFs with respect to LTRFs of different geographical regions?

MATERIALS AND METHODS

A straightforward approach to evaluate the relevance of regional history and ecological affinity in the angiosperm composition of LTRFs of Mexico would be to quantify the similarity of Mexican LTRFs with the different biomes in the regional flora, and with the flora of LTRFs at a global level, and determine which is greater. Because this direct approach has many practical complications, we obtained similarity measures among the regional and LTRF floras using different spatial units as proxies.

DATA

To compare the angiosperm composition of the LTRFs of Mexico with the regional flora, and with the flora of LTRFs at a global level, the complete species composition of the regional and the biome floras are necessary. A list of the vascular plant species of Mexico has been compiled from an intensive revision of the published literature (Villaseñor & Ortiz, 2013). The identity of each reported species has been continuously verified through corroboration with its original description and with specimens housed at the National Herbarium of Mexico (MEXU). This bibliographic search includes the revision of over 250 floristic inventories; over 350 fascicles of floras, for example, *Flora del Bajío y Regiones Adyacentes* (>160 fascicles; Rzedowski, 1991 onwards), *Flora de Veracruz* (>135 fascicles; Castillo Campos, 1980 onwards), and *Flora del Valle de Tehuacán-Cuicatlán* (>65 fascicles; Medina Lemus, 1993 onwards); and of taxonomic revisions at genus and species level. Altogether, the number of floristic and taxonomic studies on which the vascular plant species list of Mexico is based exceeds 2000. The vascular plant species list is arranged as a database that combines the taxonomic information of each species (e.g., accepted nomenclature, synonyms, membership in higher taxa) with ecological and geographic information, including growth form, occupied biome(s), and geographical distribution (Villaseñor & Ortiz, 2013). This database is continuously updated as new taxonomic, ecological, or geographical information becomes available.

The number and delimitation of biomes in Mexico vary widely among different authors (e.g., Miranda & Hernández X, 1963; Rzedowski, 1978; Challenger, 1998). Here we follow Villaseñor and Ortiz (2013), who delimited five major biome types, each comprising several more narrowly defined units that have been used by different authors: (1) humid montane forests (HMFs), comprising cloud forests, deciduous forests, *Liquidambar* L. forests, mesophytic mountain forests, temperate evergreen forests, temperate rainforests, and tropical humid mountain forests; (2) seasonally dry tropical forests (SDTFs), comprising dry tropical forests, low tropical deciduous

forests, and thorn forests; (3) temperate forests (TEMs), comprising fir forests, oak-pine forests, and pine forests; (4) tropical humid forests (THUs), comprising evergreen rainforests, semi-evergreen forests, tropical rainforests, and tropical wet forests; and (5) xerophytic scrublands (XERs), comprising alpine scrublands, chaparrals, and cold desert and hot desert scrublands. In this study, the species-level composition of the five Mexican (i.e., "regional") biomes, including the LTRFs, are based on Villaseñor and Ortiz (2013).

A list of species in LTRFs at a global level would represent the ideal counterpart to the floristic data available for Mexico, but in spite of intensive taxonomic and ecological work conducted in LTRFs around the globe, there are substantial impediments to compiling such a list. For example, regional floras (e.g., *Flora Malesiana* [floramalesiana.org/index.html]; *Flora Neotropica* [Zanoni, 1967 onwards]) include taxa that are present in multiple biomes, not just LTRFs; the biome(s) occupied by each species may not be reported, and if biomes are reported, their definitions may vary among floras. Potential species synonyms in different LTRFs would alter the total count of species. Ecological inventory plot data are increasingly available for LTRFs on a global scale (e.g., the RAINFOR network, <http://www.rainfor.org>), but in most cases, they represent partial inventories because they usually include only woody plants above a certain diameter threshold (usually 10 cm). Given these issues, we used complete species checklists of angiosperms of local LTRFs from different geographical locations. This approach ensured that each checklist corresponds to a complete floristic inventory of an LTRF at a local level. Consequently, instead of conducting a single comparison between the flora of Mexican LTRFs and the flora of LTRFs at a global level, pairwise comparisons between the LTRFs of Mexico and each of the local LTRFs were established (see below). Because independent comparisons were established, the potential existence of synonyms in different floras was not problematic. Floristic inventories of 13 LTRFs were obtained from electronic databases or compiled by us: three from Central America, eight from South America, and two from Africa (Table 1). Spelling of taxonomic names was homogenized, and each species was assigned to a family and order according to APG III (APG, 2009) and Stevens (2009). The numbers of families and species in each local flora were obtained (Table 1). This information represents the primary data on which analyses are based.

UNITS OF COMPARISON

Clades. Comparisons among floras are usually based on the presence and/or relative abundance of species. The comparisons we intend to establish involve floras from different biomes in the same geographical region (i.e., within Mexico), and from the same biome from different geographical locations (i.e., around the globe). In any of these comparisons, the number of shared species is likely to be small, thus biasing similarity measures toward low values. Furthermore, some comparisons (see below) require the phylogenetic placement of the compared units to be known precisely. The unavailability of a species-level angiosperm phylogeny is an important obstacle to establishing similarity comparisons on the basis of evolutionary history of species. Hence, we used clades above the species level as units of comparison. Genera were considered as potential units of comparison, but rejected because some may be paraphyletic, and because a genus-level phylogeny for angiosperms is also unavailable. Families were selected as comparison units because, as defined by APG III (APG, 2009) and Stevens (2009), they are monophyletic groups; precise and well-supported information about phylogenetic relationships among most angiosperm families is available (e.g., APG, 2009; Stevens, 2009; Soltis et al., 2011); and family-level clades are likely to have accumulated signatures of evolutionary history relevant to the types of questions

TABLE 1. Lowland tropical rainforest (LTRF) floras compared in this study. For each flora, the source of the species list, number of APG III-defined families (APG, 2009), and number of species are indicated.

LTRF flora	Country	Source	Number of families	Number of species
Barro Colorado	Panama	Tropicos, Missouri Botanical Garden (J. Solomon)	125	1385
Bilsa	Ecuador	Tropicos, Missouri Botanical Garden	119	1178
Central French Guiana	French Guiana	S. Mori	133	2013
Cocha Cashu	Peru	R. Foster	109	1306
Ducke	Brazil	M. Hopkins (Reserva Ducke)	118	2022
Dzanga Sangha	Central African Republic	D. Harris	113	1140
Fortuna	Panama	Missouri Botanical Garden (G. McPherson)	125	1593
Gabon	Gabon	J. Wieringa	148	4339
Iquitos	Peru	Tropicos, Missouri Botanical Garden (J. Solomon)	148	3277
Jatun Sacha	Ecuador	Tropicos, Missouri Botanical Garden (J. Solomon)	145	2540
La Selva	Costa Rica	Organization for Tropical Studies (<http://www.ots.ac.cr/index.php?option=com_content&task=view&id=162&Itemid=348>)	131	1819
LTRFs of Mexico	Mexico	J. L. Villaseñor	191	5127
Poço das Antas	Brazil	H. de Lima	94	763
Yasuni	Ecuador	Tropicos, Missouri Botanical Garden (J. Solomon)	138	3042

that we are addressing. The "abundance" of each family was quantified as the number of species belonging to that family in the evaluated flora.

Phylogenetic levels. To complement family-level clades, phylogenetic levels were also used as units of comparison. A phylogenetic level is defined here as the set of clades that share the same number of branching events between the onset of their diversification into living species (i.e., their crown node) and the root of the tree (Fig. 2). Phylogenetic levels are not monophyletic groups: the members of a particular phylogenetic level are not necessarily each other's closest relatives, nor are they of the same age. However, they are equivalent in the number of phylogenetic branching events that separate the onset of their diversification from the root of the angiosperm tree, i.e., they are equivalent in their degree of "derivedness." The phylogenetic level indicates the amount of phylogenetic splitting that took place before the diversification of a selected clade. To quantify it, a stable phylogenetic hypothesis of the full group is necessary. An angiosperm family-level phylogeny is used here, obtained through manual compilation of APG III (APG, 2009) and Stevens (2009), with supplementary information about relationships within Malpighiales (Korotkova et al., 2009). The phylogenetic level (PL) to which each APG III-delimited family belongs was determined by counting the number of nodes separating its crown node from the root of the family-level angiosperm phylogenetic tree, which corresponds to phylogenetic level zero (PL0; Fig. 2). Considering the extraordinary efforts to resolve phylogenetic relationships within angiosperms (e.g., Soltis et al., 2011), it is reasonable to assume that still-unresolved family relationships represent hard polytomies (i.e., that two or more phylogenetic branching events took place

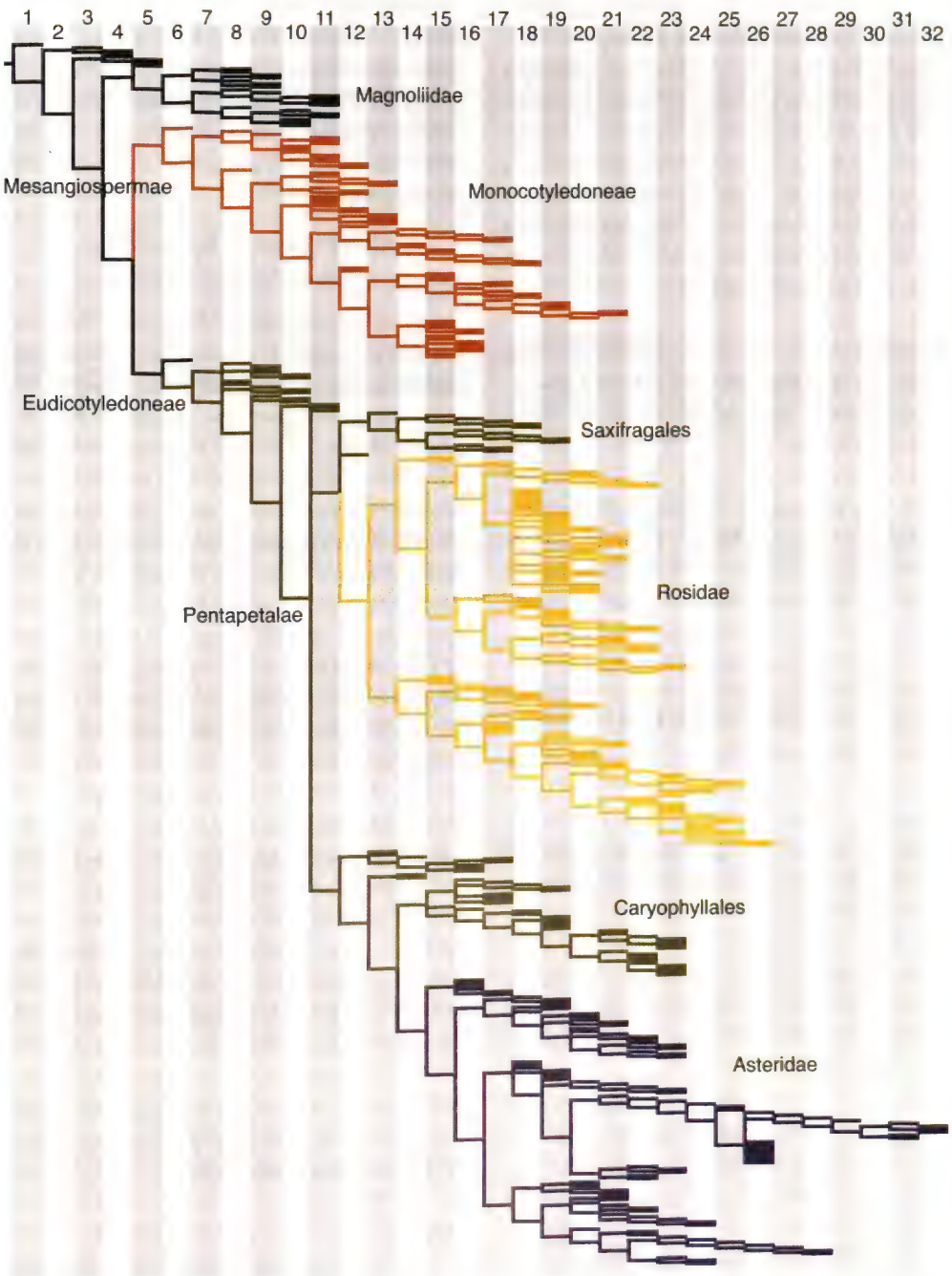
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32
Magnoliidae
Mesangiospermae
Monocotyledoneae
Eudicotyledoneae
Saxifragales
Rosidae
Pentapetalae
Caryophyllales
Asteridae

FIGURE 2. Family-level angiosperm tree drawn with equal-sized branches, reflecting the phylogenetic level of each family. The terminal node represents the crown node of each family. Compiled from order-level trees and information in Stevens (2009) and APG (2009).

in a short evolutionary time, and the sequence of branching into sister pairs can no longer be deciphered). Thus, we counted them as a single step when establishing phylogenetic levels. Comparisons among different floras were based on the number of species in each family belonging to a given phylogenetic level. The families contained in each phylogenetic level at a global scale, and the absolute and relative number of species in each, are listed in Appendix 1.

Similarity measures. The degree of similarity among floras was estimated with the altGower dissimilarity measure, as implemented in the Vegan package (Oksanen et al., 2010) in the R software environment. The altGower index is derived from Gower's general coefficient of similarity (Gower, 1971; Lim & Khoo, 1985). It is a quantitative measure as it considers the abundance of compared units, and is asymmetric as it considers shared absences to be irrelevant (Oksanen et al., 2010). The altGower index is defined as

$$d[jk] = (1 - NZ) \text{ sum } (\text{abs } (x[ij] - x[ik])),$$

where $d[jk]$ is the dissimilarity measure between localities j and k; $x[ij]$ and $x[ik]$ correspond to the abundance of species i in localities j and k, respectively; and NZ is the number of nonzero columns excluding double absences (Anderson et al., 2006; Oksanen et al., 2014). In this study, each flora corresponds to a locality, and the number of species of a family in a flora corresponds to the abundance of that family. We obtained the altGower dissimilarity index among the regional floras (corresponding to the floras of the five biomes of Mexico recognized by Villaseñor and Ortiz [2013]) and among the biome floras (i.e., the LTRF floras from different geographical locations) by establishing pairwise comparisons among all. We then considered the dissimilarity measures calculated for the LTRFs of Mexico, and recorded whether its greatest similarities are with a regional flora from a different biome, or with an LTRF from a different geographical location.

Identification of distinctive components. To identify the elements that characterize a given flora we used an overrepresentation–underrepresentation index (OUI) based on the difference between the relative abundance of a class in the evaluated flora and the relative abundance of the same class in the compared flora:

$$\text{OUI} = \%\ \text{class}_i \text{ in evaluated flora} - \%\ \text{class}_i \text{ in compared flora},$$

where classes correspond to families, and their relative abundance is determined by the percentage of species in that family with respect to the total number of species in that flora. The OUI results in values that range from positive to negative. Those classes (i.e., families) with the highest positive OUI are recognized as being overrepresented in the evaluated flora, and those with the greatest negative values are identified as most underrepresented. We established two types of comparisons: To identify distinctive families in the LTRFs of Mexico with respect to the regional flora, we identified and summarized the overrepresented families with respect to each of the four other regional biomes. To identify distinctive families in the LTRFs of Mexico with respect to the biome flora, overrepresented families in the LTRFs of Mexico were identified with respect to the LTRF floras from different geographical locations.

To further evaluate differential historical components in the LTRFs of Mexico, we also identified overrepresented phylogenetic levels in the LTRFs of Mexico with respect to other LTRF floras. Specifically, we aimed to identify if the LTRFs of Mexico contain a differential amount of "derived" or "ancestral" lineages with respect to LTRF floras from other geographical regions, particularly from South America.

RESULTS

FLORISTIC SIMILARITY OF THE LTRFS-M

The altGower dissimilarity measures obtained from pairwise comparisons among floras of the

same region and the same biome are shown in Table 2. The LTRFs-M were found to be most similar to the regional humid montane forest (HMF-M; altGower = 0.2098), followed by the geographically close LTRFs of La Selva, Costa Rica (altGower = 0.2301), and Barro Colorado, Panama (altGower = 0.2496). The lowest levels of similarity were found with the regional xerophytic scrubland (XER; altGower = 0.4035) and the LTRF of Dzanga Sangha, Central African Republic (altGower = 0.4302).

DISTINCTIVE ELEMENTS

Distinctive families in the LTRFs-M with respect to regional biomes. On average, the most overrepresented families in the LTRFs-M with respect to other biomes in the same region are Orchidaceae (OUI_x = 3.84), Rubiaceae (OUI_x = 3.33), and Piperaceae (OUI_x = 1.49), and also include Fabaceae (OUI_x = 0.96), Arecaceae (OUI_x = 0.96), and Araceae (OUI_x = 0.90) (Table 3). Asteraceae is by far the most underrepresented family in the LTRFs-M with respect to other biomes in the same region (OUI_x = –9.04). Other underrepresented families are Cactaceae (OUI_x = –2.55), Lamiaceae (OUI_x = –1.85), and Poaceae (OUI_x = –1.03).

Distinctive families in the LTRFs-M with respect to LTRFs from different locations. The families with the highest and lowest OUI values with respect to the 13 LTRF floras from other geographical locations are shown in Appendix 2. On average, the most overrepresented families in the LTRFs-M with respect to other LTRFs include Asteraceae (OUI_x = 1.96), Fabaceae (OUI_x = 1.68), Orchidaceae (OUI_x = 1.54), Bromeliaceae (OUI_x = 0.61), and Euphorbiaceae (OUI_x = 0.57); (Table 4). The most underrepresented families include, for example, Araliaceae (OUI_x = –1.19), Araceae (OUI_x = –1.16), Meliaceae (OUI_x = –1.01), Sapotaceae (OUI_x = –0.91), Rubiaceae (OUI_x = –0.74), and Moraceae (OUI_x = –0.72) (Table 4).

Distinctive phylogenetic levels in the LTRFs-M with respect to LTRFs from different locations. Phylogenetic levels with the highest average OUI values (OUI_x) for the LTRFs-M with respect to other LTRFs are PL24 (OUI_x = 3.91) and PL12 (OUI_x = 3.08) (Table 5). PL24 includes Asteraceae, and PL12 includes Orchidaceae. As indicated above, these two families were found to be overrepresented with respect to other LTRFs, and to other regional biomes, respectively.

DISCUSSION

HISTORICAL AND ECOLOGICAL DETERMINANTS OF THE COMPOSITION OF MEXICAN LOWLAND TROPICAL RAINFORESTS

The LTRFs-M are most similar to the regional humid montane forests (HMFs)—a flora from a different biome in the same geographical region. Among the regional biomes, HMFs share important environmental parameters with LTRFs, as both develop under high precipitation and humidity, and both lack a marked seasonality. They differ in their altitudinal range and annual mean temperature. In many cases, there is a physical continuum between these two biomes, from a typical LTRF at low altitude, with a gradual change in composition as altitude increases and temperature diminishes, into a typical HMF. The high floristic similarity at the family level between the regional HMFs and LTRFs reflects a shared regional history, but also ecological affinity, as both biomes develop under overlapping physical conditions. After the HMFs-M, the floras most similar to the LTRFs-M are LTRFs from other relatively close locations, namely La Selva, Costa Rica, and Barro Colorado, Panama. This result indicates the relevance of ecological affinity as an underlying cause of the composition of the LTRFs-M, and also a strong regional influence, as both floras are geographically close to the LTRFs-M, and to a certain extent, share a geological history (Ferrusquía-Villafranca, 1993;

TABLE 2. AltGower dissimilarity measures among Mexican floras of different biomes (i.e., regional floras), and LTRF floras of different geographical locations (i.e., LTRF floras). Lower altGower values indicate greatest similarity. AltGower dissimilarity measures of LTRFs-M with respect to other LTRF floras and other regional floras are in bold.

	Barro Colorado	Bilsa	CF Guiana	Cocha Cashu	Ducke	Dzanga Sangha	Fortuna	Gabon	Iquitos	Jatun Sacha	La Selva	HMFs-M	TEMs-M	LTRFs-M	SDTFs-M	XERs-M	Poço das Antas
Bilsa	0.4712																
CF Guiana	0.3509	0.4182															
Cocha Cashu	0.3440	0.5433	0.3585														
Ducke	0.4260	0.5879	0.2698	0.4343													
Dzanga Sangha	0.5252	0.6927	0.5129	0.5236	0.5575												
Fortuna	0.5696	0.3660	0.5266	0.6470	0.6941	0.7405											
Gabon	0.4111	0.5440	0.4090	0.4705	0.4776	0.2804	0.6044										
Iquitos	0.3362	0.4826	0.2373	0.2803	0.2493	0.4147	0.5823	0.4038									
Jatun Sacha	0.3145	0.3237	0.2326	0.2984	0.3749	0.4680	0.4240	0.3908	0.2596								
La Selva	0.2754	0.3428	0.3019	0.3677	0.4788	0.5699	0.4163	0.4351	0.3602	0.2205							
HMFs-M	0.3797	0.3984	0.3694	0.4378	0.4868	0.5093	0.4095	0.4073	0.4481	0.3425	0.3288						
TEMs-M	0.4504	0.5744	0.4990	0.5493	0.5697	0.5802	0.5810	0.4817	0.5464	0.4873	0.4586	0.2335					
LTRFs-M	**0.2497**	**0.3472**	**0.2751**	**0.3127**	**0.3920**	**0.4302**	**0.3987**	**0.3195**	**0.3385**	**0.2635**	**0.2301**	**0.2099**	**0.3415**				
SDTFs-M	0.4076	0.5764	0.5001	0.4965	0.5501	0.5256	0.5941	0.4424	0.4977	0.4743	0.4453	0.2771	0.2538	**0.2792**			
XERs-M	0.5353	0.6704	0.5936	0.5903	0.6482	0.6211	0.6883	0.5535	0.5784	0.5537	0.5467	0.3411	0.1968	**0.4035**	0.2783		
Poço das Antas	0.4754	0.7046	0.4480	0.5132	0.4585	0.6649	0.8089	0.5442	0.3692	0.4701	0.5643	0.5063	0.5930	**0.3911**	0.5349	0.6570	
Yasuni	0.3199	0.4155	0.2394	0.2804	0.3033	0.4466	0.5179	0.4130	0.1646	0.1670	0.2892	0.4127	0.5335	**0.3234**	0.4927	0.5835	0.4415

Abbreviations: HMFs-M = humid montane forests of Mexico; TEMs-M = temperate forests of Mexico; LTRFs-M = lowland tropical rainforests of Mexico; SDTFs-M = seasonally dry tropical forests of Mexico; XERs-M = xerophytic scrublands of Mexico.

TABLE 3. Over- and underrepresented families in the lowland tropical rainforests of Mexico (LTRFs-M) with respect to regional floras corresponding to different biomes. Positive OUI values indicate an overrepresented family, and negative OUI values indicate underrepresented family. The 20 most overrepresented and underrepresented families in the LTRFs-M with respect to each regional flora are listed. Families with the highest and lowest average OUI values are listed in the column at the extreme right. Biome delimitations are according to Villaseñor and Ortiz (2013).

	HMFs		TEMs		SDTFs		XERs			
	Family	OUI	Family	OUI	Family	OUI	Family	OUI	Family	Average OUI
1	Fabaceae	3.37	Rubiaceae	3.87	Orchidaceae	5.74	Orchidaceae	7.34	Orchidaceae	3.84
2	Rubiaceae	1.46	Orchidaceae	3.30	Rubiaceae	3.62	Rubiaceae	4.37	Rubiaceae	3.33
3	Euphorbiaceae	1.41	Piperaceae	1.71	Melastomataceae	1.75	Piperaceae	2.19	Piperaceae	1.49
4	Acanthaceae	1.03	Acanthaceae	1.29	Piperaceae	1.58	Melastomataceae	2.05	Melastomataceae	1.22
5	Bignoniaceae	0.96	Fabaceae	1.27	Primulaceae	1.14	Bromeliaceae	1.37	Primulaceae	1.03
6	Malvaceae	0.72	Melastomataceae	1.25	Arecaceae	1.04	Lauraceae	1.35	Bignoniaceae	0.96
7	Sapindaceae	0.69	Euphorbiaceae	1.20	Lauraceae	1.03	Primulaceae	1.34	Fabaceae	0.96
8	Poaceae	0.67	Primulaceae	1.15	Myrtaceae	0.93	Araceae	1.31	Arecaceae	0.96
9	Annonaceae	0.58	Myrtaceae	1.13	Araceae	0.81	Fabaceae	1.30	Myrtaceae	0.94
10	Polygonaceae	0.56	Arecaceae	1.10	Gesneriaceae	0.66	Myrtaceae	1.27	Araceae	0.90
11	Convolvulaceae	0.52	Sapindaceae	1.10	Bignoniaceae	0.66	Bignoniaceae	1.17	Sapindaceae	0.85
12	Arecaceae	0.52	Bignoniaceae	1.07	Annonaceae	0.63	Arecaceae	1.16	Acanthaceae	0.85
13	Primulaceae	0.50	Araceae	0.98	Sapindaceae	0.57	Sapindaceae	1.06	Annonaceae	0.73
14	Piperaceae	0.49	Annonaceae	0.81	Urticaceae	0.49	Gesneriaceae	1.00	Lauraceae	0.68
15	Araceae	0.49	Moraceae	0.74	Moraceae	0.47	Acanthaceae	0.96	Moraceae	0.59
16	Malpighiaceae	0.47	Apocynaceae	0.74	Salicaceae	0.43	Annonaceae	0.88	Gesneriaceae	0.59
17	Apocynaceae	0.46	Lauraceae	0.68	Celastraceae	0.41	Moraceae	0.78	Celastraceae	0.49
18	Myrtaceae	0.44	Malvaceae	0.66	Heliconiaceae	0.35	Celastraceae	0.67	Salicaceae	0.45
19	Moraceae	0.38	Celastraceae	0.62	Sapotaceae	0.29	Urticaceae	0.61	Bromeliaceae	0.43
20	Sapotaceae	0.36	Gesneriaceae	0.60	Passifloraceae	0.27	Begoniaceae	0.56	Sapotaceae	0.41

(continued)

TABLE 3. *(continued)*

	HMFs		TEMs		SDTFs		XERs			
	Family	OUI	Family	OUI	Family	OUI	Family	OUI	Family	Average OUI
1	Asteraceae	–5.67	Asteraceae	–13.23	Asteraceae	–5.90	Asteraceae	–11.34	Asteraceae	–9.04
2	Lamiaceae	–1.64	Lamiaceae	–2.67	Cactaceae	–2.34	Cactaceae	–6.61	Cactaceae	–2.55
3	Fagaceae	–1.16	Asparagaceae	–1.73	Fabaceae	–2.11	Lamiaceae	–2.11	Lamiaceae	–1.85
4	Orchidaceae	–1.03	Poaceae	–1.64	Euphorbiaceae	–1.84	Boraginaceae	–2.05	Asparagaceae	–1.33
5	Apiaceae	–1.00	Cactaceae	–1.29	Malvaceae	–1.48	Poaceae	–1.84	Poaceae	–1.03
6	Rosaceae	–0.81	Fagaceae	–1.22	Poaceae	–1.33	Asparagaceae	–1.75	Crassulaceae	–0.92
7	Solanaceae	–0.61	Apiaceae	–1.18	Asparagaceae	–1.30	Brassicaceae	–1.43	Fagaceae	–0.80
8	Crassulaceae	–0.60	Crassulaceae	–1.11	Convolvulaceae	–1.13	Crassulaceae	–1.40	Apiaceae	–0.77
9	Ericaceae	–0.57	Rosaceae	–1.00	Burseraceae	–1.10	Amaranthaceae	–1.11	Boraginaceae	–0.70
10	Asparagaceae	–0.54	Orobanchaceae	–0.92	Lamiaceae	–0.99	Plantaginaceae	–0.90	Brassicaceae	–0.64
11	Orobanchaceae	–0.44	Plantaginaceae	–0.70	Boraginaceae	–0.66	Polemoniaceae	–0.84	Orobanchaceae	–0.62
12	Ranunculaceae	–0.39	Brassicaceae	–0.68	Amaranthaceae	–0.59	Orobanchaceae	–0.82	Plantaginaceae	–0.60
13	Lauraceae	–0.34	Caryophyllaceae	–0.64	Crassulaceae	–0.58	Onagraceae	–0.75	Rosaceae	–0.56
14	Iridaceae	–0.30	Iridaceae	–0.63	Plantaginaceae	–0.54	Nyctaginaceae	–0.71	Ranunculaceae	–0.39
15	Onagraceae	–0.29	Ranunculaceae	–0.53	Commelinaceae	–0.39	Fagaceae	–0.69	Caryophyllaceae	–0.39
16	Plantaginaceae	–0.27	Onagraceae	–0.46	Malpighiaceae	–0.37	Caryophyllaceae	–0.65	Onagraceae	–0.39
17	Symplocaceae	–0.27	Caprifoliaceae	–0.45	Apiaceae	–0.33	Rhamnaceae	–0.64	Polemoniaceae	–0.38
18	Caprifoliaceae	–0.24	Polygalaceae	–0.43	Amaryllidaceae	–0.32	Apiaceae	–0.58	Rhamnaceae	–0.34
19	Clethraceae	–0.24	Polemoniaceae	–0.39	Nyctaginaceae	–0.31	Loasaceae	–0.53	Amaranthaceae	–0.31
20	Santalaceae	–0.23	Ericaceae	–0.38	Orobanchaceae	–0.29	Rosaceae	–0.50	Iridaceae	–0.31

Abbreviations: HMFs = humid montane forests; TEMs = temperate forests; SDTFs = seasonally dry tropical forests; XERs = xerophytic scrublands.

TABLE 4. Over- and underrepresented families in the lowland tropical rainforests of Mexico (LTRFs-M) with respect to LTRF floras from different geographical locations. Families with the highest and lowest average OUI values are listed (see Appendix 2 for the full list). Positive OUI values indicate an overrepresented family, and negative OUI values indicate an underrepresented family.

	Family	Average OUI	Family	Average OUI
1	Asteraceae	1.96	Araliaceae	−1.19
2	Balanophoraceae	1.76	Araceae	−1.16
3	Fabaceae	1.68	Meliaceae	−1.01
4	Orobanchaceae	1.58	Sapotaceae	−0.91
5	Orchidaceae	1.54	Ruppiaceae	−0.79
6	Fagaceae	1.26	Rubiaceae	−0.74
7	Acanthaceae	1.05	Moraceae	−0.72
8	Podostemaceae	0.85	Lecythidaceae	−0.69
9	Poaceae	0.84	Muntingiaceae	−0.65
10	Brunelliaceae	0.62	Melastomataceae	−0.62
11	Bromeliaceae	0.61	Schlegeliaceae	−0.62
12	Euphorbiaceae	0.57	Annonaceae	−0.56
13	Primulaceae	0.46	Myrtaceae	−0.53
14	Achariaceae	0.45	Apiaceae	−0.51
15	Proteaceae	0.42	Marcgraviaceae	−0.47
16	Costaceae	0.37	Colchiaceae	−0.47
17	Convolvulaceae	0.29	Clusiaceae	−0.41
18	Cytinaceae	0.26	Olacaceae	−0.39
19	Sphenocleaceae	0.23	Melianthaceae	−0.37
20	Solanaceae	0.23	Chrysobalanaceae	−0.35

Cevallos-Ferriz & González-Torres, 2005; Graham, 2010).

The floras identified as least similar to the LTRFs-M provide a counterpart to the previous pattern. The least similar flora is from the same biome, but from a distant geographical location, namely, the LTRF of Dzanga Sangha, in the Central African Republic. It is followed by a regional flora from a markedly different biome, the regional xerophytic scrubland. Thus, similarity measures indicate that both regional composition and ecological affinity are important factors underlying the angiosperm composition of the LTRFs-M.

DISTINCTIVE ELEMENTS

Families identified as overrepresented in the LTRFs-M with respect to other regional biomes, and to other LTRFs, may indicate ecological and regional influences, respectively. Overrepresented and underrepresented families are richer or more depauperate, respectively, in the LTRFs-M than would be expected given their richness in the compared flora. Considering other regional floras, families overrepresented in the LTRFs-M are mostly typical of tropical humid environments (e.g., Piperaceae, Melastomataceae, Lauraceae), and many are distinctive structural components of this biome (e.g., Arecaceae, Orchidaceae, Araceae, Bromeliaceae). Underrepresented families include some of clearly different ecological affinity (e.g., Cactaceae, Amaranthaceae, Poaceae) or of predominantly northern temperate distribution (e.g., Rosaceae, Ranunculaceae, Apiaceae).

Considering the LTRFs from elsewhere, families

TABLE 5. Overrepresented phylogenetic levels (PL) in the lowland tropical rainforests of Mexico (LTRFs-M) with respect to LTRF floras from different geographical locations. The five most overrepresented phylogenetic levels with respect to each LTRF flora are listed. Phylogenetic levels with the highest average OUI values are listed in the column at the bottom, extreme right.

	Barro Colorado		Bilsa		CF Guiana		Cocha Cashu		Ducke		Dzanga Sangha		Fortuna	
	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI
1	PL_12	3.99	PL_18	7.77	PL_24	4.82	PL_12	6.31	PL_24	5.27	PL_12	5.70	PL_18	11.51
2	PL_24	2.96	PL_20	3.91	PL_22	2.28	PL_24	3.31	PL_12	4.21	PL_24	4.93	PL_22	2.88
3	PL_10	0.81	PL_24	3.60	PL_23	1.27	PL_21	1.80	PL_22	2.56	PL_17	2.10	PL_20	2.62
4	PL_31	0.80	PL_26	1.46	PL_12	0.90	PL_23	1.42	PL_15	2.23	PL_26	1.55	PL_26	1.77
5	PL_23	0.79	PL_31	0.80	PL_31	0.57	PL_15	1.24	PL_23	1.48	PL_10	1.44	PL_24	1.42

	Gabon		Iquitos		Jatun Sacha		La Selva		Poço das Antas		Yasuni		AVERAGE	
	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI	PL	OUI
1	PL_24	4.29	PL_12	6.47	PL_24	4.10	PL_18	3.40	PL_12	8.12	PL_12	5.58	PL_24	3.91
2	PL_12	3.55	PL_24	4.94	PL_18	3.45	PL_24	2.55	PL_24	3.84	PL_24	4.82	PL_12	3.08
3	PL_09	1.86	PL_15	1.68	PL_26	1.54	PL_23	1.34	PL_20	1.49	PL_23	1.82	PL_18	0.90
4	PL_22	1.31	PL_31	1.26	PL_23	1.42	PL_12	1.19	PL_25	1.27	PL_18	1.57	PL_26	0.74
5	PL_19	1.28	PL_23	1.23	PL_12	1.37	PL_22	0.60	PL_08	1.15	PL_26	1.37	PL_23	0.74

overrepresented in the LTRFs-M include Asteraceae and Fabaceae, which are globally distributed, as well as others that are typical components of LTRFs (e.g., Orchidaceae, Acanthaceae). Underrepresented families include several with a strong ecological affinity for warm and humid environments (e.g., Araliaceae, Meliaceae, Sapotaceae, Moraceae, Lecythidaceae, Annonaceae, Clusiaceae). We emphasize that underrepresented families are not necessarily represented by few species in the LTRF-M, but their species richness is comparatively low with respect to their richness in other LTRFs.

Over- and underrepresented families may reveal regional and ecological influences. Specifically, we suggest that families whose presence in the LTRFs-M may be mostly a consequence of regional influence (i.e., they were either original components of Mexican LTRFs, or have filtered into the LTRFs-M from different regional biomes) are those that are simultaneously overrepresented with respect to LTRF floras elsewhere (Table 4), and underrepresented with respect to other regional floras (Table 3). These families are Asteraceae, Orobanchaceae, Fagaceae, and Poaceae. The first three are not typical components of LTRFs, but are of Laurasian affinity (Orobanchaceae and Fagaceae, cf. table 2 in Gentry, 1982), or are prominently represented in the flora of Mexico and adjacent latitudes (Asteraceae, Rzedowski, 1991). Families whose presence in the LTRFs-M may be largely a consequence of their ecological affinity (i.e., their presence in the LTRFs-M may be due to phylogenetic niche conservatism following movement from an LTRF in a different geographical location) are those that are simultaneously overrepresented with respect to regional floras (Table 3) and underrepresented with respect to other LTRFs (Table 4). These families are Sapotaceae, Rubiaceae, Moraceae, Melastomataceae, Annonaceae, Myrtaceae, and Araceae, some of which are characteristic components of South American LTRFs (cf. table 4 in Gentry, 1982). Families that are simultaneously overrepresented with respect to other regional floras, and to floras from the same biome are Fabaceae, Orchidaceae, Acanthaceae, Bromeliaceae, and Primulaceae (sensu APG III [APG, 2009], including Myrsinaceae and Theophrastaceae). Except for Primulaceae, these species-rich families are prominent components of South American floras. It may be postulated that, for these families, the LRTFs-M represent a site of substantial diversification, and more specifically, some may be candidates of Gondwanan ancient arrivals to the Laurasian tropics that subsequently diversified and became strongly differentiated from their South American ancestors (Gentry, 1982; see above).

DISTINCTIVE PHYLOGENETIC LEVELS

Since approximately the middle of the Cretaceous until the end of the Middle Eocene, warm conditions prevailed around the world, reaching a global thermal maximum by the Early Eocene. This global maximum was followed by a cooling trend which started in the Middle to Upper Eocene (Willis & McElwain, 2002). By the Early Eocene global thermal maximum, megathermal floras extended to high latitudes in the Northern Hemisphere, forming the so-called boreotropical flora (Wolfe, 1985; Wolfe & Upchurch, 1987; see Pennington & Dick, 2004). We expect that the Early Eocene thermal maximum left a signature in the composition of LTRFs, specifically, that clades that originated and diversified before the onset of the global cooling trend in the Upper Eocene are more prominently represented in LTRFs than clades that originated later. This prediction would be ideally tested using the absolute times of origin of major plant clades. To evaluate this hypothesis we used phylogenetic levels as a proxy to absolute time, expecting that lower and middle levels in the phylogeny might be predominant in LTRFs with respect to angiosperms as a whole. This expectation is partially confirmed, as phylogenetic levels overrepresented in LTRFs with respect to angiosperms as a whole are of intermediate level (PL20 and PL22; results not shown).

The LTRFs-M are not distinct from other LTRFs in terms of an overrepresentation of high or low phylogenetic levels. A possible exception may be PL24, which is strongly underrepresented in LTRFs with respect to angiosperms, but overrepresented in the LTRFs-M with respect to other LTRFs. PL24 includes Asteraceae (Fig. 2; Appendix 1), which is a prominent component of the Mexican flora (Rzedowski, 1991).

METHODOLOGICAL PERSPECTIVES

As far as we are aware, a standard methodology to evaluate the relative relevance of regional history and ecological affinity on the basis of whole-flora composition is not available. The relative merits of the methods we have implemented should be considered in the context of other types of information.

Data availability. Possibly the greatest obstacle to conducting comparisons of the angiosperm composition of a large geographical region that contains different biomes, and of a given biome across the globe, is obtaining complete and reliable floristic inventories that are organized according to biomes defined in a similar manner. For this study, rigorously curated information of the species composition of the regional flora was available (Villaseñor & Ortiz, 2013), but this may not be the case for other regions of similar size. A global inventory of LTRF flora is not available. Here we used checklists from several local LTRFs and conducted independent pairwise comparisons among them. A substantially larger sample of LTRFs would be desired, especially with a more comprehensive representation of African and Southeast Asian LTRFs. A promising possibility is to mine electronic biodiversity data sets (e.g., Tropicos) by filtering species that fall within a narrow envelope determined by the physical conditions of the biome of interest (e.g., precipitation, humidity, seasonality, mean annual temperature, latitudinal and altitudinal range, known geographical distribution). The group of selected species may approach a global checklist for LTRFs, although reliability of identifications and potential synonyms would still be of concern. This approach, as well as more elaborate approaches based on environmental modeling, might lend themselves better for biomes with distinct environmental preferences, such as LTRFs. It would be necessary that the parameters that delimit the biome's physical habitat are included in biodiversity datasets.

Units of comparison. In this study, we chose not to implement similarity measures at the species level because the number of shared species among different regional biomes, and among LTRFs from distant geographical localities, is likely to be very small; a species-level phylogeny of angiosperms is not available; and there are concerns about unaccounted biases. However, similarity measures that account for phylogenetic relatedness (e.g., Faith, 1992; Lozupone et al., 2007; Graham & Fine, 2008) may provide a promising alternative. Considering currently available information about phylogenetic relationships and angiosperm families at different phylogenetic levels (e.g., Soltis et al., 2011), together with analytical tools (e.g., Webb & Donoghue, 2005) and novel approaches (e.g., Morlon et al., 2011), a measure of phylogenetic relatedness among species among regional and biome floras could be obtained. Furthermore, a species-level approach could provide integrated information about patterns and events at different phases of angiosperm evolution, integrating deep time and recent speciation events.

Instead of species, we used as units of comparison clades that have been consistently recognized and are well supported in molecular phylogenies (e.g., Wang et al., 2009; Soltis et al., 2011) that have been designated as families (APG, 2009). Most living angiosperm families originated in the Upper Cretaceous or in the Tertiary, and their geographic distribution, environmental preferences, and ecological affinity should carry signatures of angiosperm evolutionary history. Nevertheless,

clades designated as families cannot be directly identified and delimited in a branching phylogeny. This requires consideration of independent information such as morphological distinctiveness, ecological function, or perhaps length of phylogenetic branches.

We also conducted comparisons using phylogenetic levels, which provide a rough assessment of the relative preponderance in different floras of groups from different stages in the angiosperm phylogeny. Alternative implementations are possible: First, to compensate for fine differences in the phylogenetic level to which a clade is assigned due to phylogenetic resolution, comparisons could be established among ranges of phylogenetic levels (e.g., PLs 1 to 5; 16 to 20). Second, levels could be established considering branch lengths in the phylogenetic tree. Each of these levels would include clades with similar amounts of relative molecular change. Finally, levels could be established on the basis of absolute time, each grouping clades that originated during a particular temporal interval (e.g., from 90 to 70 Ma; from 30 to 20 Ma) or geologic period (e.g., the Campanian, the Eocene). There is no arbitrariness in determining clade membership into a given temporal level, and these clades could represent different levels in the traditional taxonomic hierarchy. Because clades belonging to a particular temporal level originated at a given time, they are likely to carry particular signatures of geological or evolutionary history.

Similarity indices. Indices that quantify biotic similarity among communities (e.g., Sorensen, Bray-Curtis, Morisita) vary, for example, in whether they consider species abundance, the relevance of shared absences to quantify similarity, and the degree to which they are influenced by the absolute richness of the compared communities. Similarity indices that incorporate phylogenetic relatedness have been recently proposed (e.g., Lozupone et al., 2007; Graham & Fine, 2008). Incorporating phylogenetic relatedness would be an important improvement in the measure of similarity among floras, and we expect to implement this in future analyses. Similarity indices that consider phylogenetic relatedness would allow species-based comparisons, as the degree of phylogenetic relatedness would compensate for the very likely small number of shared species. Ideally, phylogenetic relatedness would be determined on the basis of a species-level phylogeny, which is not currently available for angiosperms. However, the extensive information of angiosperm relationships at all levels (e.g., Stevens, 2009), together with tools that jointly evaluate the available phylogenetic information and use it to estimate relatedness (e.g., phylomatic; Webb & Donoghue, 2005), provide feasible alternatives to measure similarities among different flora with respect to phylogeny (e.g., Morlon et al., 2011).

Overrepresentation–underrepresentation indices. The *OUI* indices implemented here are simple measures to detect classes—families in this study—that are more abundant or scarcer in a given flora with respect to other floras. The *OUI* is simple to apply and to understand, but has at least one important drawback. Because over- and underrepresented classes are detected as those with the most positive and most negative differences between the percentage of a class in the evaluated and compared floras, the classes that acquire extreme positive and negative values are also the richest overall, whereas species-poor classes will have *OUI* values close to zero. We experimented with modifying the *OUI* index by dividing it by the percentage represented by the class in the global flora—effectively penalizing classes that are extremely species-rich to be detected as over- or underrepresented in part because of their sheer richness. The results of this penalized *OUI* index were difficult to interpret because families detected as over- and underrepresented were small and lacked a distinct regional or environmental signature. Thus, for this study, we found that the unpenalized *OUI* index provided results with a

more straightforward interpretation. Simulation approaches may provide promising alternatives to identify over- and underrepresented classes. The general idea would be to model the expected richness of a class in a given flora through repeated stochastic sampling of a nesting pool, which would represent the null hypothesis. However, determining the composition of this null hypothesis (e.g., the global flora, the flora of a given biome) would require careful consideration.

Whole-flora approach. In this study, the roles of historical and ecological factors as determinants of the floristic composition of Mexican LTRFs were investigated by considering the entire composition of different floras. This whole-flora approach provides a general impression of the large-scale drivers that have shaped the present-day composition of a particular biome, but lacks sufficient resolution to differentiate the particular processes that took place, and when they happened. As such, the whole-flora approach represents a useful counterpart of clade-based studies (e.g., Richardson et al., 2001; Erkens, 2007; De-Nova et al., 2012) in which the evolutionary trajectory of a particular lineage provides information about the processes that shaped its evolution, and potentially, that of regional or biome biodiversity. Clade-based studies may recover the timing of increase or decrease in biodiversity, and potential associations with morphological evolution or with ecological or geological factors that affected a particular lineage. Although this approach provides precise indications about particular factors that possibly underlie the diversification of a lineage, the extent to which these factors also correspond to the main evolutionary processes that determined the composition of a local biome or region is unknown. Clade-based and whole-flora studies are complementary approaches that illuminate different angles of the processes that have shaped local biotas, as well as lineage-specific evolutionary factors that have affected particular clades.

SUMMARY AND CONCLUSIONS

Regional composition and ecological affinity were both found to be important factors determining the composition of Mexican LTRFs, and neither could be unequivocally distinguished as being more important. Families that characterize Mexican LTRFs with respect to the regional flora have in general greater affinity for warm and humid environments, or contain many species with growth forms that are distinctive structural components of LTRFs, specifically, families with a large number of epiphytes, as well as palms. Mexican LTRFs are mostly distinguished from LTRFs from other geographical locations by a deficit of families that are extremely species-rich in South American LTRFs. We distinguished angiosperm families that are present in Mexican LTRFs mostly as a consequence of adaptation after filtering from different regional biomes, or due to movement from LTRFs of different geographical locations as a consequence of phylogenetic niche conservatism. Mexican LTRFs seem to lack a distinctive signature of angiosperm evolution with respect to other LTRFs, possibly except for a larger-than-expected richness of Asteraceae.

Different authors have set forth ideas regarding the origin and evolutionary influences underlying the composition of northern Neotropical LTRFs. The finding that angiosperm families that are very significant components of South American, specifically Amazonian, LTRFs are less abundant than expected supports A. H. Gentry's (1982) observation regarding the diminishing abundance of Amazonian elements in lowland floras as latitude increases. A more specific question is if, as proposed by Gentry (1982), two types of South American-derived lineages can be distinguished: lineages that occupied tropical Laurasia by the end of the Cretaceous through an interrupted island arc, and which have subsequently formed tropical North American centers of diversification; and lineages that occupied North America recently, as a consequence of the closure of the Pan-

amanian isthmus, and that so far, have achieved little differentiation from their South American sources (Gentry, 1982). Our results also indicate that Mexican LTRFs contain a strong regional composition, including lineages that are characteristically Laurasian and able to withstand somewhat colder and drier conditions (i.e., Wendt, 1993). This study suggests that the floristic composition of Mexican LTRFs is the consequence of complex interactions between regional historical and ecological processes, which may have acted preferentially at different phases of its evolutionary assembly.

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APPENDIX 1. Phylogenetic levels (PL). Families contained in each phylogenetic level are indicated, including the number of species in each family and the total number of species in each phylogenetic level (in bold). Families and orders are delimited according to APG III (APG, 2009) and Stevens (2009).

PL	Order	Family	Number of species
PL01	Amborellales	Amborellaceae	1
		Total spp. PL01	**1**
PL03	Nymphaeales	Hydatellaceae	10
		Total spp. PL03	**10**
PL04	Nymphaeales	Cabombaceae	6
PL04	Nymphaeales	Nymphaeaceae	58
PL04	Austrobaileyales	Austrobaileyaceae	2
		Total spp. PL04	**66**
PL05	Austrobaileyales	Schisandraceae	92
PL05	Austrobaileyales	Trimeniaceae	6
PL05	Chloranthales	Chloranthaceae	75
		Total spp. PL05	**173**
PL06	Acorales	Acoraceae	4
PL06	Ceratophyllales	Ceratophyllaceae	6
		Total spp. PL06	**10**
PL08	Canellales	Canellaceae	13
PL08	Canellales	Winteraceae	90
PL08	Piperales	Hydnoraceae	7
PL08	Magnoliales	Myristicaceae	475
PL08	Laurales	Calycanthaceae	11
PL08	Alismatales	Araceae	4025
PL08	Petrosaviales	Petrosaviaceae	4
PL08	Ranunculales	Eupteleaceae	2
PL08	Ranunculales	Papaveraceae	760
PL08	Sabiales	Sabiaceae	100
		Total spp. PL08	**5487**
PL09	Piperales	Aristolochiaceae	480
PL09	Piperales	Lactoridaceae	1
PL09	Piperales	Piperaceae	3615
PL09	Piperales	Saururaceae	6
PL09	Magnoliales	Magnoliaceae	227
PL09	Alismatales	Tofieldiaceae	27
PL09	Ranunculales	Lardizabalaceae	36
PL09	Ranunculales	Circaeasteraceae	2
PL09	Ranunculales	Menispermaceae	420
PL09	Proteales	Nelumbonaceae	2
PL09	Trochodendrales	Trochodendraceae	2
		Total spp. PL09	**4818**
PL10	Laurales	Siparunaceae	75
PL10	Laurales	Monimiaceae	200
PL10	Laurales	Hernandiaceae	55
PL10	Laurales	Lauraceae	2500

PL	Order	Family	Number of species
PL10	Alismatales	Scheuchzeriaceae	1
PL10	Alismatales	Aponogetonaceae	43
PL10	Alismatales	Juncaginaceae	16
PL10	Ranunculales	Berberidaceae	701
PL10	Ranunculales	Ranunculaceae	2525
PL10	Proteales	Platanaceae	10
PL10	Proteales	Proteaceae	1600
PL10	Buxales	Haptanthaceae	1
PL10	Buxales	Buxaceae	72
		Total spp. PL10	**7799**
PL11	Magnoliales	Degeneriaceae	2
PL11	Magnoliales	Himantandraceae	2
PL11	Magnoliales	Eupomatiaceae	3
PL11	Magnoliales	Annonaceae	2220
PL11	Laurales	Gomortegaceae	1
PL11	Laurales	Atherospermataceae	16
PL11	Alismatales	Hydrocharitaceae	116
PL11	Alismatales	Butomaceae	1
PL11	Alismatales	Alismataceae	95
PL11	Alismatales	Posidoniaceae	9
PL11	Alismatales	Ruppiaceae	10
PL11	Alismatales	Cymodoceaceae	16
PL11	Dioscoreales	Nartheciaceae	41
PL11	Pandanales	Velloziaceae	240
PL11	Pandanales	Triuridaceae	48
PL11	Liliales	Corsiaceae	30
PL11	Liliales	Campynemataceae	4
PL11	Liliales	Melanthiaceae	170
PL11	Liliales	Petermanniaceae	1
PL11	Gunnerales	Gunneraceae	50
PL11	Gunnerales	Myrothamnaceae	2
PL11	Dilleniales	Dilleniaceae	300
		Total spp. PL11	**3377**
PL12	Alismatales	Zosteraceae	14
PL12	Alismatales	Potamogetonaceae	102
PL12	Dioscoreales	Burmanniaceae	140
PL12	Dioscoreales	Dioscoreaceae	882
PL12	Pandanales	Stemonaceae	27
PL12	Liliales	Colchiaceae	245
PL12	Liliales	Alstroemeriaceae	170
PL12	Asparagales	Orchidaceae	22,075
PL12	unplaced within Commelinidae	Dasypogonaceae	16
PL12	Arecales	Arecaceae	2361
PL12	Vitales	Vitaceae	850
		Total spp. PL12	**26,882**
PL13	Pandanales	Pandanaceae	885

(continued)

PL	Order	Family	Number of species
PL13	Pandanales	Cyclanthaceae	225
PL13	Liliales	Rhipogonaceae	6
PL13	Liliales	Philesiaceae	2
PL13	Liliales	Smilacaceae	315
PL13	Liliales	Liliaceae	610
PL13	Saxifragales	Peridiscaceae	11
PL13	Santalales	Erythropalaceae	65
PL13	Santalales	Balanophoraceae	50
		Total spp. PL13	**2169**
PL14	Asparagales	Boryaceae	12
PL14	Asparagales	Ixioliriaceae	3
PL14	Asparagales	Tecophilaeaceae	23
PL14	Berberidopsidales	Aextoxicaceae	1
PL14	Berberidopsidales	Berberidopsidaceae	3
PL14	Santalales	Olacaceae	103
		Total spp. PL14	**145**
PL15	Asparagales	Blandfordiaceae	4
PL15	Asparagales	Doryanthaceae	2
PL15	Asparagales	Iridaceae	2025
PL15	Commelinales	Commelinaceae	652
PL15	Commelinales	Hanguanaceae	6
PL15	Commelinales	Philydraceae	5
PL15	Poales	Typhaceae	25
PL15	Poales	Bromeliaceae	1700
PL15	Poales	Rapateaceae	94
PL15	Zingiberales	Musaceae	35
PL15	Zingiberales	Heliconiaceae	200
PL15	Zingiberales	Zingiberaceae	1300
PL15	Zingiberales	Costaceae	110
PL15	Saxifragales	Paeoniaceae	33
PL15	Zygophyllales	Krameriaceae	18
PL15	Zygophyllales	Zygophyllaceae	285
PL15	Geraniales	Geraniaceae	805
PL15	Geraniales	Melianthaceae	13
PL15	Geraniales	Vivianiaceae	18
PL15	Myrtales	Combretaceae	500
PL15	Caryophyllales	Rhabdodendraceae	3
		Total spp. PL15	**7833**
PL16	Asparagales	Lanariaceae	1
PL16	Asparagales	Xeronemataceae	2
PL16	Commelinales	Haemodoraceae	116
PL16	Commelinales	Pontederiaceae	33
PL16	Poales	Mayacaceae	10
PL16	Zingiberales	Strelitziaceae	7
PL16	Zingiberales	Lowiaceae	15
PL16	Zingiberales	Cannaceae	10

PL	Order	Family	Number of species
PL16	Zingiberales	Marantaceae	550
PL16	Saxifragales	Altingiaceae	13
PL16	Saxifragales	Crassulaceae	1370
PL16	Saxifragales	Iteaceae	21
PL16	Myrtales	Onagraceae	656
PL16	Myrtales	Lythraceae	620
PL16	Crossosomatales	Aphloiaceae	1
PL16	Crossosomatales	Geissolomataceae	1
PL16	Crossosomatales	Strasburgeriaceae	2
PL16	Picramniales	Picramniaceae	26
PL16	Santalales	Loranthaceae	950
PL16	Santalales	Opiliaceae	60
PL16	Santalales	Santalaceae	990
PL16	Caryophyllales	Droseraceae	115
PL16	Caryophyllales	Simmondsiaceae	1
PL16	Cornales	Hydrostachyaceae	20
PL16	Cornales	Cornaceae	107
PL16	Cornales	Hydrangeaceae	190
PL16	Cornales	Loasaceae	265
		Total spp. PL16	**6152**
PL17	Asparagales	Asteliaceae	36
PL17	Asparagales	Hypoxidaceae	220
PL17	Asparagales	Xanthorrhoeaceae	900
PL17	Poales	Xyridaceae	260
PL17	Poales	Eriocaulaceae	1160
PL17	Poales	Thurniaceae	4
PL17	Poales	Anarthriaceae	11
PL17	Saxifragales	Hamamelidaceae	82
PL17	Saxifragales	Aphanopetalaceae	2
PL17	Saxifragales	Grossulariaceae	150
PL17	Saxifragales	Saxifragaceae	540
PL17	Celastrales	Lepidobotryaceae	3
PL17	Celastrales	Celastraceae	1402
PL17	Fabales	Quillajaceae	3
PL17	Myrtales	Vochysiaceae	190
PL17	Myrtales	Myrtaceae	4620
PL17	Myrtales	Melastomataceae	5005
PL17	Crossosomatales	Staphyleaceae	45
PL17	Crossosomatales	Guamatelaceae	1
PL17	Santalales	Misodendraceae	8
PL17	Santalales	Schoepfiaceae	55
PL17	Caryophyllales	Nepenthaceae	90
PL17	Caryophyllales	Frankeniaceae	90
PL17	Caryophyllales	Tamaricaceae	90
PL17	Caryophyllales	Plumbaginaceae	836
PL17	Caryophyllales	Polygonaceae	1110

(continued)

PL	Order	Family	Number of species
PL17	Cornales	Grubbiaceae	3
PL17	Cornales	Curtisiaceae	1
		Total spp. PL17	**16,917**
PL18	Asparagales	Amarillidaceae	1604
PL18	Asparagales	Asparagaceae	2648
PL18	Poales	Juncaceae	430
PL18	Poales	Cyperaceae	4350
PL18	Saxifragales	Cercidiphyllaceae	2
PL18	Saxifragales	Daphniphyllaceae	10
PL18	Saxifragales	Tetracarpaeaceae	1
PL18	Oxalidales	Huaceae	3
PL18	Malpighiales	Linaceae	300
PL18	Malpighiales	Irvingiaceae	10
PL18	Malpighiales	Ixonanthaceae	21
PL18	Malpighiales	Humiriaceae	50
PL18	Malpighiales	Pandaceae	15
PL18	Malpighiales	Ochnaceae	551
PL18	Malpighiales	Centroplacaceae	6
PL18	Malpighiales	Caryocaraceae	21
PL18	Fabales	Fabaceae	19,400
PL18	Fabales	Polygalaceae	940
PL18	Fabales	Surianaceae	8
PL18	Rosales	Rosaceae	2520
PL18	Myrtales	Crypteroniaceae	10
PL18	Crossosomatales	Stachyuraceae	5
PL18	Crossosomatales	Crossosomataceae	12
PL18	Sapindales	Biebersteiniaceae	5
PL18	Sapindales	Nitratiaceae	16
PL18	Sapindales	Sapindaceae	1580
PL18	Caryophyllales	Drosophyllaceae	1
PL18	Caryophyllales	Asteropeiaceae	8
PL18	Caryophyllales	Physenaceae	2
PL18	Ericales	Balsaminaceae	1001
PL18	Ericales	Lecythidaceae	310
PL18	unplaced **within Lamiidae**	Oncothecaceae	2
PL18	unplaced **within Lamiidae**	Metteniusaceae	7
PL18	unplaced	Icacinaceae	150
		Total spp. PL18	**35,999**
PL19	Poales	Centrolepidaceae	35
PL19	Poales	Restionaceae	500
PL19	Poales	Flagellariaceae	4
PL19	Saxifragales	Penthoraceae	2
PL19	Saxifragales	Haloragaceae	145
PL19	Malpighiales	Achariaceae	145
PL19	Malpighiales	Goupiaceae	2
PL19	Malpighiales	Lophopyxidaceae	1

PL	Order	Family	Number of species
PL19	Malpighiales	Putranjivaceae	210
PL19	Malpighiales	Ctenolophonaceae	3
PL19	Malpighiales	Elatinaceae	35
PL19	Malpighiales	Malpighiaceae	1250
PL19	Malpighiales	Peraceae	135
PL19	Malpighiales	Phyllanthaceae	1745
PL19	Malpighiales	Picrodendraceae	80
PL19	Malpighiales	Balanopaceae	9
PL19	Cucurbitales	Anisophylleaceae	34
PL19	Fagales	Nothofagaceae	35
PL19	Rosales	Barbeyaceae	1
PL19	Rosales	Dirachmaceae	2
PL19	Rosales	Rhamnaceae	925
PL19	Rosales	Elaeagnaceae	45
PL19	Myrtales	Alzateaceae	2
PL19	Myrtales	Penaeaceae	29
PL19	Huerteales	Gerrardinaceae	2
PL19	Sapindales	Kirkiaceae	8
PL19	Sapindales	Rutaceae	1815
PL19	Sapindales	Meliaceae	621
PL19	Sapindales	Simaroubaceae	110
PL19	Caryophyllales	Ancistrocladaceae	12
PL19	Caryophyllales	Dioncophyllaceae	3
PL19	Caryophyllales	Caryophyllaceae	2200
PL19	Caryophyllales	Achatocarpaceae	7
PL19	Caryophyllales	Amaranthaceae	2500
PL19	Caryophyllales	Stegnospermataceae	3
PL19	Caryophyllales	Limeaceae	23
PL19	Ericales	Marcgraviaceae	130
PL19	Ericales	Tetrameristaceae	5
PL19	Ericales	Polemoniaceae	385
PL19	Ericales	Fouquieriaceae	11
PL19	Garryales	Garryaceae	17
PL19	Garryales	Eucommiaceae	1
PL19	unplaced	Boraginaceae	2740
PL19	unplaced within Lamiidae	Vahliaceae	8
		Total spp. PL19	**15,975**
PL20	Poales	Poaceae	10,035
PL20	Oxalidales	Connaraceae	180
PL20	Oxalidales	Oxalidaceae	770
PL20	Oxalidales	Cunoniaceae	280
PL20	Malpighiales	Violaceae	800
PL20	Malpighiales	Passifloraceae	934
PL20	Malpighiales	Lacistemataceae	14
PL20	Malpighiales	Salicaceae	1010
PL20	Malpighiales	Erythroxylaceae	240

(continued)

PL	Order	Family	Number of species
PL20	Malpighiales	Rhizophoraceae	149
PL20	Malpighiales	Bonneticaceae	35
PL20	Malpighiales	Clusiaceae	595
PL20	Malpighiales	Calophyllaceae	460
PL20	Malpighiales	Rafflesiaceae	20
PL20	Malpighiales	Euphorbiaceae	5735
PL20	Fagales	Fagaceae	670
PL20	Rosales	Ulmaceae	35
PL20	Huerteales	Tapisciaceae	5
PL20	Huerteales	Dipentodontaceae	16
PL20	Malvales	Neuradaceae	10
PL20	Sapindales	Anacardiaceae	600
PL20	Sapindales	Burseraceae	550
PL20	Ericales	Sladeniaceae	3
PL20	Ericales	Pentaphylacaceae	337
PL20	Ericales	Sapotaceae	1100
PL20	Ericales	Mitrastemonaceae	2
PL20	Ericales	Theaceae	460
PL20	Gentianales	Rubiaceae	13,150
PL20	Aquifoliales	Cardiopteridaceae	45
PL20	Aquifoliales	Stemonuraceae	95
PL20	Aquifoliales	Phyllonomaceae	4
PL20	Asterales	Pentaphragmataceae	30
PL20	Escalloniales	Escalloniaceae	130
		Total spp. PL20	**38,499**
PL21	Poales	Joinvilliaceae	2
PL21	Poales	Ecdeiocoleaceae	3
PL21	Oxalidales	Elaeocarpaceae	605
PL21	Malpighiales	Hypericaceae	560
PL21	Malpighiales	Podostemaceae	270
PL21	Malpighiales	Trigoniaceae	28
PL21	Malpighiales	Dichapetalaceae	165
PL21	Malpighiales	Chrysobalanaceae	460
PL21	Malpighiales	Euphroniaceae	2
PL21	Cucurbitales	Corynocarpaceae	6
PL21	Cucurbitales	Coriariaceae	5
PL21	Cucurbitales	Cucurbitaceae	845
PL21	Fagales	Myricaceae	57
PL21	Fagales	Juglandaceae	51
PL21	Rosales	Cannabaceae	170
PL21	Brassicales	Akaniaceae	2
PL21	Brassicales	Tropaeolaceae	95
PL21	Malvales	Thymelaeaceae	891
PL21	Caryophyllales	Lophiocarpaceae	6
PL21	Caryophyllales	Barbeuiaceae	1

PL	Order	Family	Number of species
PL21	Caryophyllales	Molluginaceae	87
PL21	Ericales	Ebenaceae	548
PL21	Ericales	Primulaceae	2590
PL21	Ericales	Symplocaceae	320
PL21	Gentianales	Gentianaceae	1655
PL21	Lamiales	Plocospermataceae	1
PL21	Aquifoliales	Aquifoliaceae	405
PL21	Aquifoliales	Helwingiaceae	3
PL21	Asterales	Rousseaceae	13
PL21	Asterales	Campanulaceae	2380
PL21	Asterales	Alseusomiaceae	10
PL21	Asterales	Stylidiaceae	245
		Total spp. PL21	**12,481**
PL22	Oxalidales	Brunelliaceae	55
PL22	Oxalidales	Cephalotaceae	1
PL22	Cucurbitales	Tetramelaceae	2
PL22	Cucurbitales	Datiscaceae	2
PL22	Cucurbitales	Begoniaceae	1401
PL22	Fagales	Casuarinaceae	95
PL22	Rosales	Moraceae	1100
PL22	Rosales	Urticaceae	2625
PL22	Brassicales	Moringaceae	12
PL22	Brassicales	Caricaceae	34
PL22	Brassicales	Setchellanthaceae	1
PL22	Brassicales	Limnanthaceae	8
PL22	Malvales	Sphaerosepalaceae	18
PL22	Malvales	Bixaceae	21
PL22	Malvales	Malvaceae	4225
PL22	Caryophyllales	Aizoaceae	2020
PL22	Caryophyllales	Halophytaceae	1
PL22	Caryophyllales	Didiereaceae	16
PL22	Caryophyllales	Basellaceae	19
PL22	Caryophyllales	Montiaceae	27
PL22	Ericales	Styracaceae	160
PL22	Ericales	Diapensiaceae	18
PL22	Ericales	Sarraceniaceae	15
PL22	Ericales	Clethraceae	75
PL22	Gentianales	Loganiaceae	420
PL22	Lamiales	Carlemanniaceae	5
PL22	Solanales	Montiniaceae	5
PL22	Solanales	Convolvulaceae	1625
PL22	Solanales	Solanaceae	2460
PL22	Asterales	Phellinaceae	12
PL22	Asterales	Argophyllaceae	21
PL22	Asterales	Menyanthaceae	58

(continued)

PL	Order	Family	Number of species
PL22	Bruniales	Bruniaceae	75
PL22	Bruniales	Collumeliaceae	5
		Total spp. PL22	**16,637**
PL23	Fagales	Ticodendraceae	1
PL23	Fagales	Betulaceae	145
PL23	Brassicales	Koeberliniaceae	2
PL23	Brassicales	Emblingiaceae	1
PL23	Brassicales	Pentadiplandraceae	1
PL23	Brassicales	Tovariaceae	2
PL23	Malvales	Cistaceae	175
PL23	Malvales	Cytinaceae	10
PL23	Malvales	Muntingiaceae	3
PL23	Caryophyllales	Gisekiaceae	5
PL23	Caryophyllales	Sarcobataceae	2
PL23	Caryophyllales	Phytolaccaceae	65
PL23	Caryophyllales	Nyctaginaceae	395
PL23	Caryophyllales	Talinaceae	27
PL23	Caryophyllales	Portulacaceae	100
PL23	Caryophyllales	Anacampserotaceae	32
PL23	Caryophyllales	Cactaceae	1500
PL23	Ericales	Actinidiaceae	355
PL23	Ericales	Roridulaceae	2
PL23	Ericales	Cyrillaceae	2
PL23	Ericales	Ericaceae	3995
PL23	Gentianales	Gelsemiaceae	11
PL23	Gentianales	Apocynaceae	4555
PL23	Lamiales	Oleaceae	615
PL23	Solanales	Sphenocleaceae	2
PL23	Solanales	Hydroleaceae	12
PL23	Asterales	Goodeniaceae	440
PL23	Apiales	Pennantiaceae	4
PL23	Paracryphiales	Paracryphiaceae	36
		Total spp. PL23	**12,495**
PL24	Brassicales	Bataceae	2
PL24	Brassicales	Salvadoraceae	11
PL24	Brassicales	Gyrostemonaceae	18
PL24	Brassicales	Resedaceae	75
PL24	Malvales	Capparaceae	480
PL24	Malvales	Sarcolaenaceae	60
PL24	Lamiales	Dipterocarpaceae	680
PL24	Asterales	Tetrachondraceae	3
PL24	Asterales	Calyceraceae	60
PL24	Apiales	Asteraceae	23,600
PL24	Dipsacales	Torricelliaceae	10
		Adoxaceae	200

PL	Order	Family	Number of species
PL24	Dipsacales	Caprifoliaceae	890
		Total spp. PL24	**26,089**
PL25	Brassicales	Cleomaceae	300
PL25	Brassicales	Brassicaceae	3710
PL25	Lamiales	Calceolariaceae	260
PL25	Lamiales	Gesneriaceae	3200
PL25	Apiales	Griseliniaceae	6
		Total spp. PL25	**7476**
PL26	Lamiales	Peltanthera	1
PL26	Lamiales	Pedaliaceae	70
PL26	Lamiales	Martyniaceae	16
PL26	Lamiales	Linderniaceae	195
PL26	Lamiales	Bignoniaceae	800
PL26	Lamiales	Schlegeliaceae	28
PL26	Lamiales	Acanthaceae	4000
PL26	Lamiales	Byblidaceae	6
PL26	Lamiales	Lentibulariaceae	320
PL26	Apiales	Pittosporaceae	200
		Total spp. PL26	**3150**
PL27	Lamiales	Plantaginaceae	1700
PL27	Apiales	Araliaceae	1450
		Total spp. PL27	**3150**
PL28	Lamiales	Scrophulariaceae	1700
PL28	Apiales	Myodocarpaceae	19
PL28	Apiales	Apiaceae	3780
		Total spp. PL28	**5499**
PL29	Lamiales	Stilbaceae	39
		Total spp. PL29	**39**
PL31	Lamiales	Lamiaceae	7173
PL31	Lamiales	Thomandersiaceae	6
PL31	Lamiales	Verbenaceae	1175
		Total spp. PL31	**8354**
PL32	Lamiales	Paulowniaceae	6
PL32	Lamiales	Phrymaceae	234
PL32	Lamiales	Orobanchaceae	2060
		Total spp. PL32	**2300**

APPENDIX 2. Over- and underrepresented families in lowland tropical rainforest (LTRFs) floras with respect to the lowland tropical rainforest of Mexico (LTRFs-M). Positive OUI values indicate that the family is overrepresented; negative OUI values indicate that the family is underrepresented. The 20 most overrepresented and underrepresented families in the LTRFs-M with respect to each LTRF flora are listed. Families with the average highest and lowest OUI values are listed in Table 4.

	Barro Colorado		Bilsa		CF Guiana		Cocha Cashu		Ducke	
	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI
1	Orchidaceae	4.17	Fabaceae	6.83	Asteraceae	4.29	Orchidaceae	6.57	Orchidaceae	4.86
2	Asteraceae	2.45	Poaceae	3.33	Fabaceae	2.32	Asteraceae	3.34	Asteraceae	4.79
3	Euphorbiaceae	1.78	Asteraceae	3.27	Poaceae	1.86	Fabaceae	1.93	Poaceae	2.70
4	Bromeliaceae	1.41	Euphorbiaceae	2.40	Acanthaceae	1.42	Bromeliaceae	1.88	Acanthaceae	2.17
5	Acanthaceae	1.29	Cyperaceae	1.33	Euphorbiaceae	1.15	Poaceae	1.70	Bromeliaceae	1.68
6	Primulaceae	1.01	Acanthaceae	1.07	Malvaceae	1.08	Convolvulaceae	0.98	Solanaceae	1.55
7	Verbenaceae	0.80	Myrtaceae	1.01	Solanaceae	0.90	Apocynaceae	0.96	Malvaceae	1.33
8	Lauraceae	0.58	Convolvulaceae	0.86	Primulaceae	0.80	Primulaceae	0.83	Rubiaceae	1.23
9	Convolvulaceae	0.57	Bignoniaceae	0.78	Bromeliaceae	0.78	Euphorbiaceae	0.76	Euphorbiaceae	1.21
10	Gesneriaceae	0.51	Verbenaceae	0.67	Orchidaceae	0.77	Dioscoreaceae	0.45	Primulaceae	0.90
11	Amaranthaceae	0.50	Rutaceae	0.60	Convolvulaceae	0.77	Asparagaceae	0.43	Piperaceae	0.81
12	Begoniaceae	0.45	Primulaceae	0.59	Polygonaceae	0.59	Gesneriaceae	0.40	Convolvulaceae	0.77
13	Celastraceae	0.42	Dioscoreaceae	0.52	Begoniaceae	0.56	Begoniaceae	0.36	Cyperaceae	0.72
14	Cactaceae	0.36	Amaranthaceae	0.47	Lythraceae	0.44	Cactaceae	0.35	Fabaceae	0.67
15	Asparagaceae	0.36	Malpighiaceae	0.45	Asparagaceae	0.43	Lamiaceae	0.34	Begoniaceae	0.66
16	Capparaceae	0.36	Asparagaceae	0.43	Dioscoreaceae	0.41	Lythraceae	0.33	Gesneriaceae	0.62
17	Myrtaceae	0.33	Rhamnaceae	0.37	Capparaceae	0.38	Phyllanthaceae	0.33	Lamiaceae	0.57
18	Solanaceae	0.29	Cactaceae	0.34	Apocynaceae	0.35	Verbenaceae	0.33	Amaranthaceae	0.54
19	Ericaceae	0.29	Begoniaceae	0.32	Plantaginaceae	0.34	Ericaceae	0.29	Cactaceae	0.46
20	Fagaceae	0.29	Polygonaceae	0.32	Phyllanthaceae	0.33	Fagaceae	0.29	Commelinaceae	0.46

1	Araceae	−2.46	Araceae	−7.98	Sapotaceae	−2.87	Moraceae	−3.03	Lauraceae	−3.55
2	Poaceae	−2.08	Gesneriaceae	−4.33	Melastomataceae	−1.86	Bignoniaceae	−2.54	Sapotaceae	−3.25
3	Moraceae	−1.35	Melastomataceae	−2.09	Lecythidaceae	−1.62	Sapindaceae	−2.06	Chrysobalanaceae	−2.49
4	Bignoniaceae	−1.31	Urticaceae	−1.47	Chrysobalanaceae	−1.60	Araceae	−1.62	Lecythidaceae	−2.16
5	Malpighiaceae	−0.93	Moraceae	−1.08	Lauraceae	−1.24	Annonaceae	−1.40	Clusiaceae	−2.09
6	Sapindaceae	−0.85	Clusiaceae	−1.03	Araceae	−1.24	Meliaceae	−1.26	Annonaceae	−2.02
7	Piperaceae	−0.69	Ericaceae	−0.98	Clusiaceae	−1.21	Sapotaceae	−1.23	Myrtaceae	−1.87
8	Clusiaceae	−0.68	Lecythidaceae	−0.83	Bignoniaceae	−0.95	Menispermaceae	−1.18	Burseraceae	−1.73
9	Fabaceae	−0.65	Cucurbitaceae	−0.81	Burseraceae	−0.94	Marantaceae	−1.05	Melastomataceae	−1.49
10	Dilleniaceae	−0.60	Cyclanthaceae	−0.73	Marantaceae	−0.91	Piperaceae	−0.72	Bignoniaceae	−1.43
11	Melastomataceae	−0.60	Marcgraviaceae	−0.65	Annonaceae	−0.79	Urticaceae	−0.71	Moraceae	−1.37
12	Marantaceae	−0.53	Orchidaceae	−0.62	Sapindaceae	−0.75	Myristicaceae	−0.63	Araceae	−1.28
13	Loganiaceae	−0.53	Marantaceae	−0.60	Ochnaceae	−0.66	Arecaceae	−0.59	Myristicaceae	−1.18
14	Menispermaceae	−0.52	Rubiaceae	−0.52	Loganiaceae	−0.60	Malvaceae	−0.55	Sapindaceae	−0.89
15	Malvaceae	−0.52	Meliaceae	−0.50	Moraceae	−0.53	Melastomataceae	−0.54	Meliaceae	−0.86
16	Apocynaceae	−0.48	Schlegeliaceae	−0.49	Gentianaceae	−0.53	Passifloraceae	−0.52	Arecaceae	−0.85
17	Heliconiaceae	−0.42	Solanaceae	−0.47	Rubiaceae	−0.53	Solanaceae	−0.51	Elaeocarpaceae	−0.70
18	Costaceae	−0.40	Boraginaceae	−0.47	Myrtaceae	−0.44	Nyctaginaceae	−0.47	Ochnaceae	−0.65
19	Connaraceae	−0.39	Myristicaceae	−0.45	Elaeocarpaceae	−0.41	Acanthaceae	−0.47	Dilleniaceae	−0.58
20	Passifloraceae	−0.38	Passifloraceae	−0.40	Vochysiaceae	−0.41	Lecythidaceae	−0.44	Polygalaceae	−0.57

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	Dzanga Sangha		Fortuna		Gabon		Iquitos		Jatun Sacha	
	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI
1	Orchidaceae	5.74	Fabaceae	8.65	Asteraceae	4.03	Orchidaceae	7.47	Asteraceae	3.75
2	Asteraceae	4.69	Poaceae	2.65	Orchidaceae	2.57	Asteraceae	4.57	Fabaceae	3.00
3	Poaceae	2.70	Euphorbiaceae	2.40	Bromeliaceae	2.42	Poaceae	2.35	Poaceae	1.68
4	Bromeliaceae	2.42	Malvaceae	1.83	Piperaceae	2.09	Bromeliaceae	1.87	Bromeliaceae	1.51
5	Piperaceae	2.17	Apocynaceae	1.78	Solanaceae	1.87	Acanthaceae	1.72	Convolvulaceae	1.05
6	Solanaceae	1.89	Convolvulaceae	1.30	Bignoniaceae	1.13	Fabaceae	1.45	Euphorbiaceae	0.99
7	Primulaceae	1.44	Sapindaceae	1.26	Myrtaceae	1.02	Cyperaceae	1.11	Primulaceae	0.93
8	Myrtaceae	1.26	Asteraceae	1.21	Primulaceae	1.01	Verbenaceae	0.94	Orchidaceae	0.88
9	Fabaceae	1.19	Cyperaceae	1.06	Gesneriaceae	0.92	Convolvulaceae	0.88	Acanthaceae	0.86
10	Melastomataceae	1.01	Bignoniaceae	0.85	Poaceae	0.92	Euphorbiaceae	0.78	Apocynaceae	0.81
11	Gesneriaceae	1.01	Acanthaceae	0.76	Arecaceae	0.84	Solanaceae	0.78	Verbenaceae	0.66
12	Lauraceae	1.00	Myrtaceae	0.66	Boraginaceae	0.84	Primulaceae	0.71	Cyperaceae	0.61
13	Verbenaceae	1.00	Celastraceae	0.62	Lauraceae	0.68	Begoniaceae	0.60	Begoniaceae	0.51
14	Convolvulaceae	0.93	Annonaceae	0.46	Convolvulaceae	0.67	Amaranthaceae	0.55	Bignoniaceae	0.46
15	Bignoniaceae	0.85	Amaranthaceae	0.46	Polygonaceae	0.60	Piperaceae	0.51	Dioscoreaceae	0.45
16	Araceae	0.74	Moraceae	0.45	Malpighiaceae	0.60	Asparagaceae	0.43	Amaranthaceae	0.41
17	Polygonaceae	0.74	Asparagaceae	0.43	Urticaceae	0.50	Lythraceae	0.37	Asparagaceae	0.39
18	Boraginaceae	0.71	Polygonaceae	0.43	Lythraceae	0.49	Plantaginaceae	0.36	Boraginaceae	0.38
19	Acanthaceae	0.67	Rutaceae	0.42	Cactaceae	0.48	Cactaceae	0.35	Lythraceae	0.33
20	Arecaceae	0.62	Verbenaceae	0.40	Araceae	0.45	Lamiaceae	0.32	Plantaginaceae	0.31

1	Rubiaceae	−8.28	Orchidaceae	−7.10	Rubiaceae	−7.09	Annonaceae	−2.92	Araceae	−3.32
2	Annonaceae	−2.35	Araceae	6.72	Annonaceae	−2.03	Moraceae	−1.76	Moraceae	−1.88
3	Apocynaceae	−2.05	Melastomataceae	−2.89	Apocynaceae	−1.46	Lauraceae	−1.67	Melastomataceae	−1.67
4	Putranjivaceae	1.61	Ericaceae	−2.78	Dichapetalaceae	−1.44	Araceae	−1.67	Rubiaceae	−1.55
5	Moraceae	−1.59	Rubiaceae	−2.61	Cyperaceae	−1.29	Sapotaceae	−1.62	Sapotaceae	−1.29
6	Phyllanthaceae	−1.34	Piperaceae	−2.30	Combretaceae	−1.12	Sapindaceae	−1.36	Myristicaceae	−1.04
7	Zingiberaceae	−1.33	Gesneriaceae	−1.62	Celastraceae	−1.06	Arecaceae	−1.33	Lauraceae	−1.04
8	Meliaceae	−1.24	Cyclanthaceae	−1.39	Zingiberaceae	−1.05	Chrysobalanaceae	−1.29	Gesneriaceae	−0.91
9	Sapotaceae	−1.24	Musaceae	−1.05	Loganiaceae	−0.93	Clusiaceae	−1.22	Clusiaceae	−0.89
10	Combretaceae	1.23	Clusiaceae	−0.99	Violaceae	−0.86	Myristicaceae	−1.19	Meliaceae	−0.87
11	Ochnaceae	−1.18	Solanaceae	−0.90	Sapotaceae	−0.85	Rubiaceae	−1.18	Marantaceae	−0.85
12	Malvaceae	−1.17	Marcgraviaceae	−0.76	Ochnaceae	−0.83	Burseraceae	−1.08	Annonaceae	−0.84
13	Marantaceae	−1.16	Marantaceae	−0.74	Moraceae	−0.75	Menispermaceae	−1.04	Solanaceae	−0.71
14	Sapindaceae	−1.16	Zingiberaceae	−0.68	Icacinaceae	−0.72	Lecythidaceae	−0.93	Urticaceae	−0.68
15	Lamiaceae	−1.12	Arecaceae	−0.62	Connaraceae	−0.69	Meliaceae	−0.91	Menispermaceae	−0.67
16	Connaraceae	−1.11	Urticaceae	−0.56	Fabaceae	−0.63	Melastomataceae	−0.86	Lecythidaceae	−0.57
17	Commelinaceae	1.06	Loranthaceae	−0.55	Ebenaceae	−0.63	Marantaceae	−0.80	Chrysobalanaceae	−0.51
18	Celastraceae	1.02	Araliaceae	−0.48	Begoniaceae	−0.63	Malpighiaceae	−0.65	Burseraceae	−0.36
19	Menispermaceae	−0.96	Campanulaceae	−0.48	Olacaceae	−0.59	Bignoniaceae	−0.60	Loganiaceae	−0.32
20	Achariaceae	−0.86	Chloranthaceae	−0.36	Putranjivaceae	−0.59	Ochnaceae	−0.57	Vochysiaceae	−0.32

(continued)

	La Selva		Poço das Antas		Yasuni	
	FAMILY	OUI	FAMILY	OUI	FAMILY	OUI
1	Fabaceae	3.59	Fabaceae	3.59	Orchidaceae	5.50
2	Asteraceae	2.40	Asteraceae	2.40	Asteraceae	4.40
3	Orchidaceae	1.57	Orchidaceae	1.57	Fabaceae	2.64
4	Euphorbiaceae	0.84	Euphorbiaceae	0.84	Poaceae	1.90
5	Verbenaceae	0.82	Verbenaceae	0.82	Bromeliaceae	1.47
6	Celastraceae	0.77	Celastraceae	0.77	Euphorbiaceae	1.29
7	Bromeliaceae	0.77	Bromeliaceae	0.77	Acanthaceae	1.20
8	Convolvulaceae	0.76	Convolvulaceae	0.76	Verbenaceae	0.90
9	Apocynaceae	0.75	Apocynaceae	0.75	Convolvulaceae	0.87
10	Primulaceae	0.67	Primulaceae	0.67	Cyperaceae	0.83
11	Polygonaceae	0.52	Polygonaceae	0.52	Apocynaceae	0.73
12	Acanthaceae	0.48	Acanthaceae	0.48	Primulaceae	0.65
13	Solanaceae	0.43	Solanaceae	0.43	Dioscoreaceae	0.51
14	Plantaginaceae	0.39	Plantaginaceae	0.39	Begoniaceae	0.43
15	Begoniaceae	0.39	Begoniaceae	0.39	Asparagaceae	0.43
16	Myrtaceae	0.36	Myrtaceae	0.36	Lythraceae	0.42
17	Fagaceae	0.29	Fagaceae	0.29	Amaranthaceae	0.41
18	Salicaceae	0.29	Salicaceae	0.29	Piperaceae	0.40
19	Asparagaceae	0.26	Asparagaceae	0.26	Plantaginaceae	0.39
20	Campanulaceae	0.22	Campanulaceae	0.22	Cactaceae	0.34

1	Araceae	–4.38	Araceae	–4.38	Araceae	–2.90
2	Melastomataceae	–2.06	Melastomataceae	–2.06	Melastomataceae	–2.21
3	Piperaceae	–1.45	Piperaceae	–1.45	Lauraceae	–2.11
4	Clusiaceae	–0.99	Clusiaceae	–0.99	Rubiaceae	–1.63
5	Marantaceae	–0.82	Marantaceae	–0.82	Sapotaceae	–1.53
6	Cyclanthaceae	–0.82	Cyclanthaceae	–0.82	Annonaceae	–1.50
7	Moraceae	–0.80	Moraceae	–0.80	Moraceae	–1.48
8	Gesneriaceae	–0.69	Gesneriaceae	–0.69	Myristicaceae	–1.09
9	Arecaceae	–0.65	Arecaceae	–0.65	Sapindaceae	–1.08
10	Urticaceae	–0.56	Urticaceae	–0.56	Meliaceae	–1.02
11	Zingiberaceae	–0.53	Zingiberaceae	–0.53	Chrysobalanaceae	–0.92
12	Cucurbitaceae	–0.49	Cucurbitaceae	–0.49	Menispermaceae	–0.91
13	Poaceae	–0.45	Poaceae	–0.45	Burseraceae	–0.87
14	Scrophulariaceae	–0.44	Scrophulariaceae	–0.44	Clusiaceae	–0.82
15	Lamiaceae	–0.43	Lamiaceae	–0.43	Marantaceae	–0.69
16	Heliconiaceae	–0.40	Heliconiaceae	–0.40	Lecythidaceae	–0.61
17	Meliaceae	–0.29	Meliaceae	–0.29	Arecaceae	–0.58
18	Sapotaceae	–0.27	Sapotaceae	–0.27	Urticaceae	–0.53
19	Marcgraviaceae	–0.27	Marcgraviaceae	–0.27	Combretaceae	–0.51
20	Costaceae	–0.26	Costaceae	–0.26	Gesneriaceae	–0.50

FRUITS OF *MELIA* (MELIACEAE, MELIOIDEAE) FROM THE MIDDLE MIOCENE YAKIMA CANYON FLORA OF CENTRAL WASHINGTON STATE, U.S.A.

Kathleen B. Pigg, Melanie L. DeVore, John C. Benedict, and Richard M. Creekmore*

ABSTRACT

Melia yakimaensis Pigg, DeVore, Benedict & Creekmore (Meliaceae, Melioideae) is described for permineralized endocarps from the Middle Miocene Yakima Canyon flora of central Washington State, U.S.A. Fruits are scleritized endocarps, 2.8–3.7 mm long and 3.2–3.6 mm across, with prominent vertical ridges, a flattened base and a pointed apex. They are 5- to 9-loculate with subapical, axile placentation, and they bear a single, pendulous, mature seed and sometimes several small, presumably abortive seeds per locule. They provide some of the first evidence of Meliaceae subfam. Melioideae in the western North American Neogene and contribute to our understanding of the floristic diversity of the Middle Miocene Yakima Canyon "bog" flora.

Key words: Columbia River Basalt Group, drupe, Melioideae, permineralization, septicidal dehiscence.

The Meliaceae is a family of mostly tropical and subtropical trees and shrubs of Old and New World distribution. Authors have recognized variously two, four, or five subfamilies, with the previous most authoritative treatments recognizing four subfamilies, including Melioideae and Swietenioideae, and the monotypic genera *Quivisianthe* Baill. and *Capuronianthus* J.-F. Leroy (Pennington & Styles, 1975; Mabberley, 2011). Phylogenetic analyses of Meliaceae, based on nuclear and plastid DNA sequences (Muellner et al., 2003, 2006) including representatives of all four subfamilies, supported only Melioideae and Swietenioideae; *Quivisianthe* was placed in Melioideae and *Capuronianthus* in Swietenioideae, which is recognized as Cedreloideae in the most recent taxonomic treatment of the family (Mabberley, 2011). The traditional subfamily Melioideae includes genera with fleshy fruits and seeds lacking wings, such as the chinaberry, *Melia* L., which are typically bird- and fruit bat-dispersed (White, 1986; Voigt et al., 2011). Subfamily Cedreloideae contains taxa with capsules and winged seeds that are wind-dispersed, such as *Swietenia* Jacq. (mahogany) and *Cedrela* P. Browne.

Except for the fossil wood record, particularly of the mahoganies, the fossil record of the family is not extensively distributed; however, it does also

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include flowers, fruits, seeds, possible leaves, and pollen. Leaf and fertile remains are from North America and Europe, and wood occurs in Europe, Africa, India, and North America. Of the two currently recognized subfamilies, members of Cedreloideae presumably are more common in the fossil record, although some of these reports are in need of confirmation. Among the megafossil remains attributable to the family, the most commonly recognized forms in the western North American Tertiary are those of the genus *Cedrela* (Manchester, 2001).

In the current study we describe permineralized endocarps of *Melia* L. from the Middle Miocene Yakima Canyon flora of central Washington State, U.S.A. (Pigg & DeVore, 2005). This material is the oldest known anatomically preserved fruit record of the genus and documents subfamily Melioideae in the Neogene of western North America, where subfamily Cedreloideae is known already from the Paleogene (e.g., *Cedrela*).

MATERIALS AND METHODS

Most of the specimens were collected from 1965 to 1990 by T. H. Tuggle and Raymond D. Foisy from the Middle Miocene Yakima Canyon area in Yakima County, central Washington State, between the cities of Yakima and Ellensburg (Burke Museum of Natural History and Culture, University of Washington, Seattle, locality number B4101). Two specimens were found in a collection made in 1993 by the authors. Fossils were recovered from the sites referred to locally as the "County Line Holes," primarily from the area within the site designated "Hi Hole" by the original collectors (Pigg & DeVore, 2005).

The fossils are found within the Columbia River Basalt Group. Previously we stated that they occur within interbeds of the Sentinel Bluffs Unit of the Grand Ronde Basalt within the Museum Flow Package of N_2 Grand Ronde Basalt, which is dated 15.6 million years old by argon-argon (Ar/Ar) dating (Borgardt & Pigg, 1999). Reevaluation of the deposition demonstrates that fossils are found directly within pockets in the basalt flow and not within an interbed (Pigg & DeVore, 2005). Recently obtained dates from the adjacent basalts confirm this previously determined age (Pigg et al., 2007). Specimens that comprise part of the Tuggle/Foisy collection were borrowed from the Burke Museum of Natural History and Culture, University of Washington (UWBM), while other material is housed in the Paleobotanical Collections, School of Life Sciences, Arizona State University (ASU).

Specimens were examined with a Nikon (Melville, New York, U.S.A.) SMZ-10 dissecting microscope and photographed prior to sectioning. Several specimens were sectioned at intervals of 35 µm with a Microslice 2 annular diamond saw (Ultratec, Santa Ana, California, U.S.A.) with a paper-thin diamond blade, and others were wafered at thicker intervals on a Buehler IsoMet Low Speed Saw (Ultratec). Sections were mounted onto microscope slides with either epoxy or UV-cured adhesive with coverslips mounted in xylene-soluble Permount adhesive (Thermo Fisher Scientific, Inc., Anthem, Arizona, U.S.A.) and studied with reflected and/or transmitted light. Extant endocarps of *Melia azedarach* L. were sectioned freehand or embedded in Ward's bioplastic and wafered on the Buehler IsoMet Low Speed Saw.

SYSTEMATICS

Family: Meliaceae Juss.

Subfamily: Melioideae Arn.

Genus: *Melia* L.

Species: ***Melia yakimaensis*** Pigg, DeVore, Benedict & Creekmore, sp. nov.

Holotype: designated here: Specimen 8, UWBM 56470-50 (Fig. 1H, 2A, E–G).

Paratypes: designated here: Specimen 2, UWBM 56479-7 (Fig. 1E, F); Specimen 5, UWBM 56470-41 (Fig. 1I); Specimen 6, UWBM 56479-15 (Fig. 1A–C); Specimen 9, UWBM 56488 (Fig. 2B); Specimen 12, ASUYC (Arizona State University Yakima Canyon) 59 (Fig. 2C); Specimen 13, ASUYC 60 (Fig. 3A, D). Not figured: Specimen 1, UWBM 56479-14; Specimen 3, UWBM 56470-39; Specimen 4, UWBM 56479-12; Specimen 7, UWBM 56479-6; Specimen 10, UWBM 56478-3; Specimen 11, UWBM 56470.

Type Locality: "Hi Hole" County Line Holes, Yakima Canyon, Washington.

Stratigraphy and age: Columbia River Basalt Group, Middle Miocene.

Referred material: "Capsule-like fruit," figures 53–55 in Pigg and Wehr (2002).

Etymology: The specific epithet, *yakimaensis*, refers to the collecting locality in Yakima Canyon, Washington State, U.S.A.

Species diagnosis: Endocarps turbinate (top-shaped) to spherical, 2.8–3.7 × 3.2–3.6 mm, 5- to 9-loculate; with prominent vertical ridges marking central rib of locule from base to apex; endocarp tissue highly sclerotic, placentation axile with seeds attached subapically; seeds flattened, ovate, with elongated hilar region, one mature seed per locule; fruits septicidal, splitting into pyrenes.

Description: This description is based on a total of 13 specimens of fossil endocarps (Figs. 1A–C, E, F, H, I, 2A–C, E–G, 3A, D) that greatly resemble the fruits that we examined of extant *Melia azedarach* (Meliaceae) (Figs. 1D, G, J–L, 2D, H, 3B, C). Of these, 10 specimens were found in the round, weathered out from the matrix (Figs. 1A–C, E, F, H, I, 2A, E–G). These specimens include five complete fruits, four half fruits (the result of weathering and septicidal dehiscence), and one almost complete fruit with a single pyrene removed. Three specimens occur within the chert matrix on weathered surfaces, one oriented in slightly oblique transverse section (Fig. 2B) and the others in oblique longitudinal section (Figs. 2C, 3A, D). Some specimens have a complete fruit axis like those seen in extant endocarps (Figs. 1A–C, 2A, C), while others have a central hollow area corresponding to the central fruit axis (Figs. 1F, I, 2B).

Fruits are 2.8–3.7 × 3.2–3.6 mm, generally turbinate (top-shaped) with the apical half of the fruit extending to a pointed apex (Figs. 1A, E, 3A) and the basal half broader and somewhat flattened at the base (Fig. 1B, H). There is some variation in this general shape, with some endocarps tending toward spherical (Fig. 1E) or vertically flattened (Fig. 1B). Similar variation is seen among extant endocarps, with more tending toward obovate (Fig. 1K). The fruit axis, 0.5 mm in diameter, is seen in some specimens (Figs. 1C, 2A), as in extant forms (Fig. 1L). Prominent vertical ridges that expand in the central part of each locule extend from the fruit apex to the base (Fig. 1A–C, E, H).

Fruits are 5- to 9-loculate endocarps with axile placentation (Fig. 2A–C). The central axis of the endocarps, when preserved, is typically star-shaped, around 500 μm in diameter, and contains a central pith of darker, resinous material (Fig. 2A) that apparently contains bubbles upon fossilization (Fig. 2E). Each locule has a prominent central ridge to the outside and bears a single mature seed that is aligned along the same radius as the central ridge (Figs. 2A–C, 3A). Some specimens have smaller, presumably abortive seeds (Fig. 2C) like those seen in extant fruits (Fig. 2D). Seeds are borne subapically along the central axis and are pendulous within the locule (Fig. 3A, D), as in extant forms (Fig. 3B). The endocarp is composed of highly scleritized, elongate, thick-walled cells with simple pits throughout (macrosclereids) (Fig. 2F). They tend to be aligned somewhat radially, but occur in a swirling pattern around the

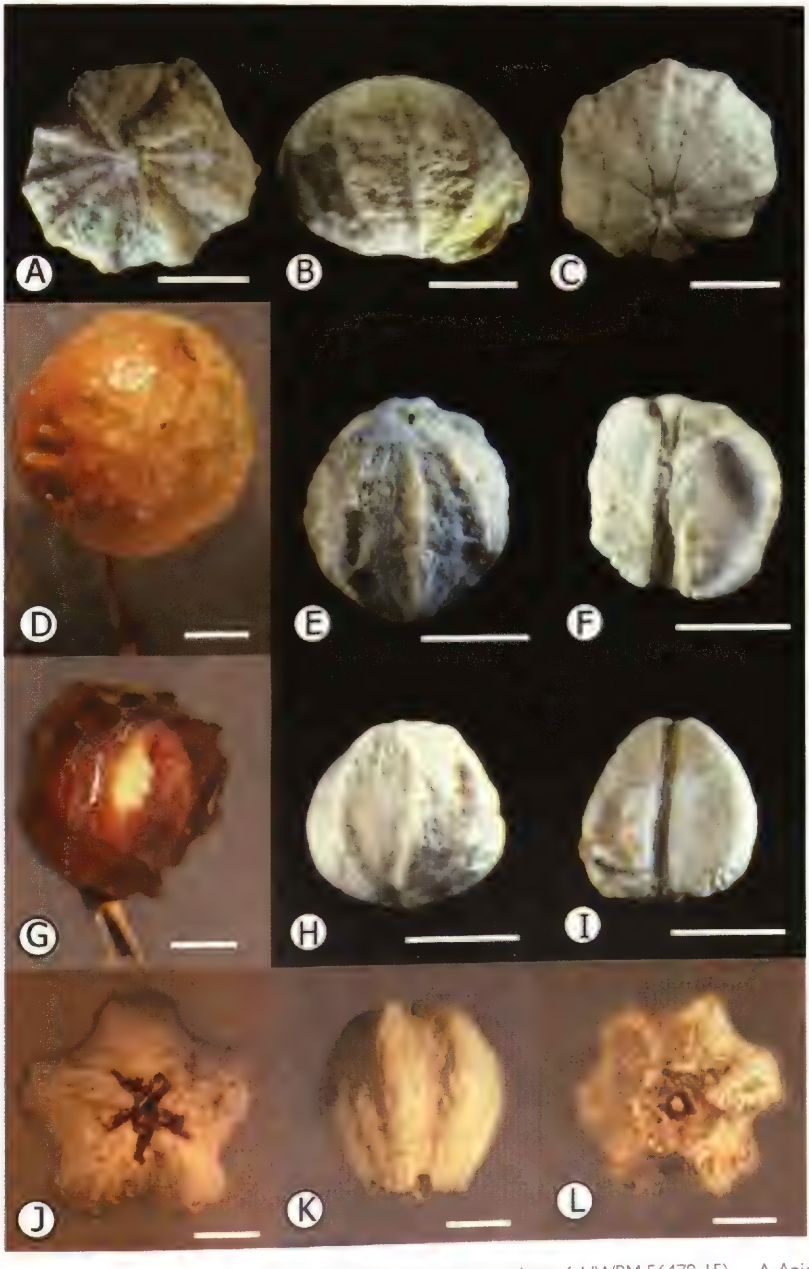

FIGURE 1. Fossil and extant *Melia* fruits. A–C. Fossil *M. yakimaensis* fruit (specimen 6, UWBM 56479-15). —A. Apical view. —B. Side view. —C. Basal view. —D. Extant *M. azedarach* L. fruit complete with external pericarp intact. E, F. Fossil *M. yakimaensis* fruit (specimen 2, UWBM 56479-7). —E. Outside. —F. Inside. —G. Extant *M. azedarach* fruit with partially degraded pericarp, revealing endocarp below. —H. Fossil *M. yakimaensis* fruit (holotype, specimen 8, UWBM 56470-50). —I. Fossil *M. yakimaensis* fruit (specimen 5, UWBM 56470-41). J–L. Extant *M. azedarach* fruits corresponding to fossil views in A–C. —J. Apical view. —K. Side view. —L. Basal view. Scale bars: A–C = 2 mm; D = 1.5 mm; E = 2.5 mm; F = 2.6 mm; G = 1.5 mm; H = 2.7 mm; I = 2.6 mm; J–L = 1.5 mm.

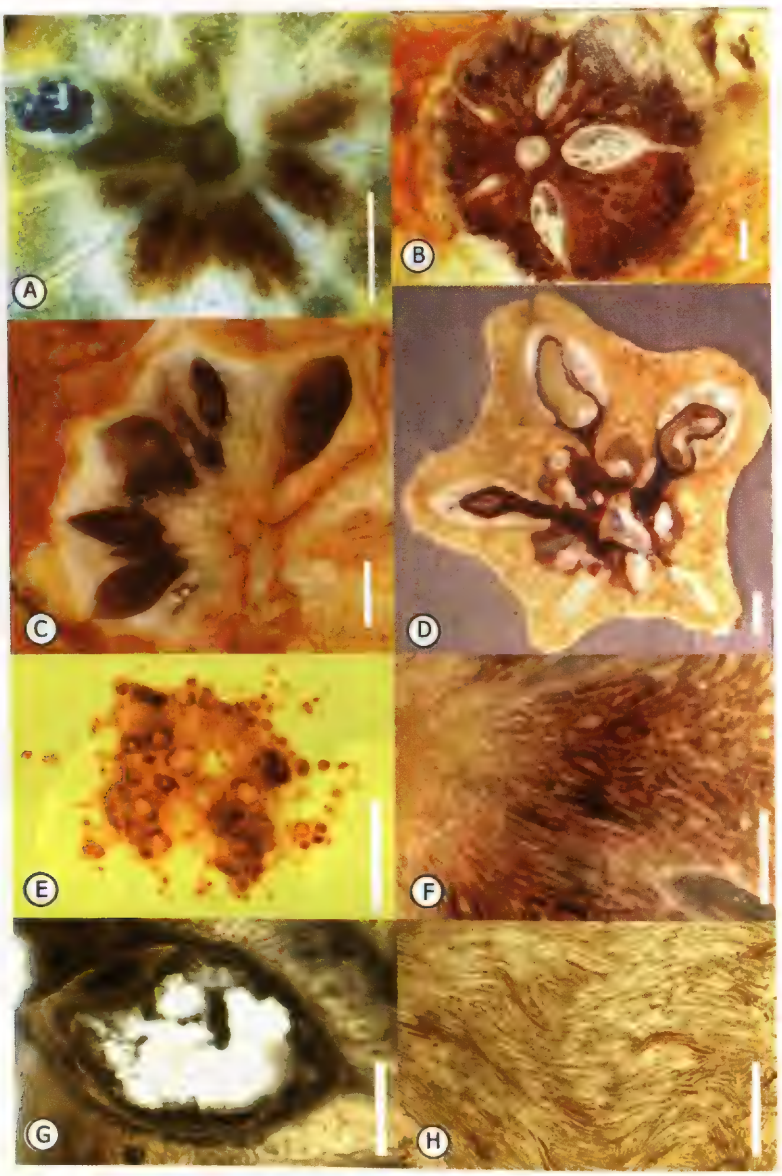

FIGURE 2. Fossil and extant *Melia azedarach* L. fruits, transverse sections and anatomical detail. A–C. Fossil *M. yakimaensis*. —A. Transverse section showing pith, radiating lines showing position of septa, and highly scleritized fruit wall; note seed at upper left (holotype, specimen 8, UWBM 56470-50). —B. Fossil fruit in surface of chert matrix showing hollow central axis and seeds aligned along septa (specimen 9, UWBM 56488). —C. Fossil fruit in transverse section, cut at level fairly close to fruit apex, with large (maturing) and small (presumably aborted) seeds near point of attachment (specimen 12, ASUYC 59. #3Top). —D. Extant fruit of *M. azedarach*, transverse section cut at level near fruit apex with numerous seeds in attachment, both large (maturing) and small (presumably aborted). Note dark amorphous material in fruit axis. E–G. Fossil fruits, anatomical details of *M. yakimaensis* holotype. —E. Detail of pith in Figure 2A, showing bubblelike structures. —F. Detail of highly sclerified endocarp, showing distribution of sclereids swirling around top edge of seed (appearing as horizontal line). —G. Detail of seed. —H. Extant *M. azedarach* endocarp, detail showing organization of sclereids. Scale bars: A = 2.7 mm; B = 1 mm; C = 1.6 mm; D = 1 cm; E = 2.8 mm; F, G = 2.4 mm.

seeds (Fig. 2A, F), in a manner similar to that in extant *Melia* (Fig. 2H).

Seeds are 2.4 × 0.6 mm and flattened, with a straight edge facing the axis and a curved margin to the outside (Figs. 2G, 3A, D) like those of extant *Melia* (Fig. 3C). Like their modern counterparts, they have an elongated hilar region (Fig. 3A, D).

DISCUSSION

ASSIGNMENT TO *MELIA*

Fossil endocarps of *Melia yakimaensis* can be assigned easily to *Melia*, a distinctive member of Meliaceae subfam. Melioideae, on the basis of their fruit and seed characters. These include the general fruit organization as small endocarps with prominent vertical ridges; a locule number of five to nine; the subapical attachment of seeds; the highly sclerotic nature of the endocarp; the presence of dark, presumably resinous material in the central axis; and the general shape of the seeds with their distinctive elongate hilar region.

Extant *Melia* fruits are initially drupes, with a fleshy mesocarp and waxy exocarp (Fig. 1D). These outer layers are broken, eaten, and/or mechanically degraded to reveal a highly scleritized, septicidal endocarp (Fig. 1G, J–L). Upon weathering, endocarps eventually split septicidally, usually into either half fruits or, occasionally, with individual locules separating from one another as pyrenes (or mericarps). Our observations of extant *Melia* show that endocarps eventually become free of the fleshy mesocarp after weathering for some months to a year or more. The Yakima Canyon fossils are of fruit endocarps from which the fleshy mesocarp has degraded completely. As in extant *Melia* endocarps, in *M. yakimaensis* the central axis of the fruit may be present (Fig. 1A–C, 2A, E) or sometimes is completely degraded, leaving a hollow center (Fig. 1F, I, 2B, 3A). This hollow central area apparently provides a plane of weakness that contributes to the mechanical splitting of the endocarps upon weathering.

FIGURE 3. Fossil and extant *Melia*. —A. Fossil *M. yakimaensis*, oblique longitudinal section through fruit in matrix, showing several seeds in longitudinal view and fruit apex, at top (specimen 13, ASUYC 60). —B. Extant fruit of *M. azedarach* L., longitudinal section near level of apex, showing subapical attachment of several abortive seeds. Note elongate hilar attachment. —C. Extant fruit of *M. azedarach*, longitudinal section through locule, showing elongate hilar attachment of seeds. —D. Fossil *M. yakimaensis*, detail of Figure 3A, showing seeds with elongate hilar attachment. Scale bars: A = 1.7 mm; B = 2 mm; C = 0.8 mm; D = 1.4 mm.

The endocarps of the fossils, like those of the extant forms, are highly scleritized, with five to nine 1-seeded locules (Fig. 2B, D). Fruits also have a centrally placed, radially aligned dehiscence slit along the main rib of each locule, suggesting loculicidal dehiscence might also occur on occasion. However, we have seen no evidence of dehisced fruits or isolated seeds. It is more likely that the dehiscence slit is a remnant of a similar feature that is functional in related fruits that are loculicidally dehiscent capsules.

Fruits of *Melia* are distinctive from the other drupes in Meliaceae, which are known in *Azadirachta* A. Juss. and *Owenia* F. Muell. They differ from these fruits in locule number, endocarp type, and seed coat. In contrast to *Melia* drupes that typically have a highly scleritized endocarp and five to nine 1-seeded locules, *Azadirachta* fruits have 1- or sometimes 2-seeded drupes with a thin, cartilaginous endocarp and seeds with thin, membraneous seed coats (Mabberley et al., 1995). *Owenia* fruits are 2- to 3-locular drupes with thin, fleshy, or leathery mesocarps and thick, hard, woody endocarps. In contrast to extant *Melia*, *M. yakimaensis* endocarps are considerably smaller, roughly one half the size of those in living fruits. They also tend to be more turbinate to spherical in shape, while groups of extant endocarps we studied were more often obovate.

Melia has been recognized variously as having a single to several species (Mabberley, 2011). Cheek (1989) recognized three species, noting differences in fruit and seed characters in each. In comparison to Cheek's (1989) delimitation, the fruits and seeds of *M. yakimaensis* show a combination of morphological characters found in individual "species." Endocarps of *M. yakimaensis* are generally most similar in overall isodiametric shape to specimens recognized by Cheek (1989) as *M. azedarach*, in comparison to the elongate fruits he placed in *M. dubia* Cav. and material designated as *M. volkensii* Gürke. *Melia yakimaensis* also has the characteristic star-shaped stele seen in *M. azedarach* sensu Cheek (1989) (Fig. 2L), and in general, seeds appear similar. Several features of *M. dubia* sensu Cheek (1989) are also seen in the fossil *M. yakimaensis*, namely the curved and attenuated region of hilar attachment and a pronounced domelike apical tip of the radicle, as well as a tendency to produce several abortive ovules per fruit (Fig. 2C, D). *Melia volkensii* sensu Cheek (1989) shows both sterile, multiloculate fruits, and those with a single viable seed.

Seed development (Nair, 1959) and anatomy (Netolitsky, 1936; Vaughn, 1970; Corner, 1976; Cheek, 1989) have been described for extant *Melia* with seeds being formed from bitegmic ovules, primarily from the testa (outer integument). In this context, the *M. yakimaensis* seed coat appears more similar to that of *M. azedarach* sensu Cheek (1989), and it lacks the prominent palisade layer of forms that have been designated by Cheek (1989) as *M. dubia.*

FOSSIL RECORD OF MELIACEAE AND *MELIA*

The oldest fossil fruits to be assigned to the Meliaceae are known from the Maastrichtian of Wyoming, Montana, and Saskatchewan, and the Dakota Formation of Kansas (Hollick, 1903). These fossils were described originally as *Ficus* L. (Knowlton, 1911) and later as *Guarea* F. Allam. ex L. (Graham, 1962; Shoemaker, 1977). From our cursory examination of specimens housed in the Museum of Paleontology, University of Michigan, and other specimens given to us by William C. Rember, University of Idaho, we could not conclude with certainty how to interpret them, since they lack the morphological and/or anatomical features needed to be identifiable unequivocally to Meliaceae.

Fruits and seeds described from the Late Cretaceous of Senegal were assigned to Meliaceae and considered to be similar to the genera *Carapa* Aubl. and *Trichilia* P. Browne (Monteillet & Lappartient, 1981). These specimens need to be reevaluated; they cannot be identified on the basis of this report, because there are no photographs

in the publication to demonstrate the nature of the specimens.

Tertiary fruit and seed occurrences of Meliaceae are found in the Early Eocene London Clay Formation flora, where fruits are attributed to *Toona* (Endl.) M. Roem. (Reid & Chandler, 1933; Collinson, 1983). These fruits clearly belong to the Meliaceae, and presumably to subfamily Cedreloideae, based on their prominent winged seeds; however, their generic assignment is in need of reevaluation (Pigg et al., 2007; Pigg & DeVore, 2010). Pyritized fruits of *Melicarya* Reid & Chandler from the London Clay bear some similarities with Meliaceae; however, they lack the combination of features present in extant genera, and may not belong to the family (Steven R. Manchester, Florida Museum of Natural History, pers. comm., February 2013).

Anatomically preserved fruits compared with *Cedrela* and *Toona* have been recognized recently in the Late Eocene flora of Post, Oregon (Manchester & McIntosh, 2007). The winged seeds of *Cedrela* and related leaves are well-known compression/impression fossils from the Late Eocene Florissant flora of Colorado (MacGinitie, 1953; Manchester, 2001; Meyer, 2003) and the Oligocene of Montana (Becker, 1961, 1962). Leaves from the Florissant flora have been assigned to *Trichilia* by MacGinitie (1953) and are listed without comment in Manchester's (2001) revision of the Florissant megafossil flora. A leaf referred to *Toona* has been reported from the Middle Eocene of Alaska. This report is in need of reevaluation (Wolfe, 1977). Flowers of *Swietenia* have been described in Late Oligocene–Early Miocene amber of Mexico (Castañeda-Posadas & Cevallos-Ferriz, 2007). Fossil endocarps assignable to *Melia* occur in the Miocene of Poland (Czeczott et al., 1959, 1961) and from the Early Pleistocene of Japan (Tsukagoshi et al., 1997) and the Pleistocene of Thailand (Grote, 2007).

Fossil pollen of Meliaceae has been reviewed by Muller (1981), and interested readers should consult this paper for details. He accepts *Guarea* from the Oligocene of Puerto Rico (Graham & Jarzen, 1969); *Psilastephanocolporites grandis* Wingate & Nichols (compared with *Trichilia*) from the Oligocene of Cameroon (see Muller, 1981); and *Meliopollis* Wingate & Nichols from Middle Tertiary sites in western North America (Wingate & Nichols, 2001). He accepted "cf. *Melia*" cf. *azedarach* (Salard-Cheboldaeff, 1978) as attributable to Meliaceae but not unequivocally to the genus *Melia*. More recent pollen occurrences since Muller (1981) include the Late Oligocene of Ethiopia (Danehy, 2010; Aaron Pan, Southern Methodist University, pers. comm., April 2013).

The fossil wood record for Meliaceae, including the mahoganies, has been compiled in the online compendium InsideWood (2004 onwards). Wood anatomy of Meliaceae has been carefully investigated since the timbers of the family are of considerable economic importance (Kribs, 1930; InsideWood, 2004 onwards; Gregory et al., 2009). Wood in Meliaceae sometimes may be distinctive at infrafamilial levels (Kribs, 1930; InsideWood, 2004 onwards). From a taxonomic standpoint, because of the many genera with overlapping wood anatomical features, using wood anatomical features alone to consistently delimit genera of extant Meliaceae is not possible (Mabberley, 2011). In this context, it is not possible to authoritatively place fossil wood types into modern genera.

FRUIT AND SEED DISPERSAL IN MELIACEAE

Within the subfamily Melioideae, fruits in more derived clades are capsules with seeds with fleshy outgrowths originating from localized or generalized meristematic regions of the outer integument (i.e., arils; Corner, 1976; Cheek, 1989). However, the basalmost members have drupes with endocarps that are either hard, or thin and membraneous (*Azadirachta*), and that may split septicidally to produce pyrenes as dispersal units. In contrast, all other members of the Melioideae have seeds that are the principal dispersal units.

Clearly, selection for dispersal has played a major role in the diversification of extant taxa. Furthermore, the role of attraction may not be the sole feature selected for. The Meliaceae contain an impressive array of secondary compounds; fruit evolution may be a balance between attraction of biotic dispersal agents and defense against herbivory (Mulholland et al., 2000).

The much smaller size of the fossil endocarps in comparison to extant *Melia* endocarps (roughly half) is intriguing. Taxa with larger-sized, fleshy fruits have been shown to attract fewer, more specialized species of avian dispersers than do other arboreal plants with smaller, fleshy fruits (McKey, 1975; Howe & Estabrook, 1977; Wheelwright, 1985). Birds with larger beaks, and consequently larger gapes, will eat both small and large fruits, while birds with smaller gapes are capable of dispersing only small fruits. In studies of interactions between bat and bird dispersers of introduced *Melia* in South Africa, Voight and colleagues (2011) documented dispersal of *Melia* fruits by seven species of birds and one species of bats. Of these, the dark-capped bulbul was capable of dispersing propagules into suitable microsites. Clearly, increasing fruit size would decrease the number of bat and bird dispersers of *Melia* propagules. However, field observations (Voight et al., 2011) demonstrate that the genus is capable of linking into local plant dispersal webs where it has been introduced. The potential for documenting a trend for increase of fruit size of *Melia* can only be fully addressed if additional reports of the genus in the fossil record are made in the future.

A second, perhaps stronger, source of evidence for animal-plant relationships of *Melia* can be drawn from the anatomy of the fruits themselves. The Meliaceae have an impressive array of secondary compounds. In *Melia* alone, terpenoids, steroids, alkaloids, flavonoids, anthraquinones, and a variety of other compounds have been isolated. The genus is best known for the production of limonoids, which are tetranortriterpenoids with a b-substituted furanyl ring at C(17) (Zhao et al., 2010). Antifeeding insect compounds and growth inhibitors are present within *Melia*'s chemical arsenal, as are other compounds with antibacterial, antiviral, and antifungal activities (Zhao et al., 2010). There are reports of poisoning in humans and pigs, but not in birds, sheep, or goats (Mabberley, 2011). Of these studies, some focus on the extracts of the endocarp. In one study (Wandscheer et al., 2004) a connection was made between the pigmented, dark brown testa and the ability to obtain active compounds from the seeds themselves. Bioassays using only the cotyledons found an active larvicidal compound obtained from the cotyledons. However, the production of the dark material (extant) and resinous material present in the pith of the endocarp's central axis suggests that this region of the fruit would likely be a source of secondary compounds. Both fossil and extant *Melia* have dark, amorphous, and presumably resinous material in the pith (Fig. 2A, D, E). The anatomy of fossil *Melia* suggests that the endocarp had evolved the ability to produce an array of secondary compounds by the Miocene.

Although the fossil record of fruits and seeds in Meliaceae is scant, we note that the occurrence of capsules with winged seeds in the Early Eocene London Clay (*Toona*) and *Cedrela* in Eocene and Oligocene of western North America is consistent with the basal appearance of subfamily Cedreloideae. The presence of *Melia* in the Miocene of Washington State documents that drupes with endocarps appeared by the Neogene in western North America, and essentially modern *Melia* was present by the Pleistocene in Thailand (Grote, 2007). What the fossil record cannot address is how the complexity of fruit types evolved within Meliaceae and the rates of evolution within the family. As new fossil materials become available for description, and as more paleobotanists recognize that members of the family represented in the Paleogene record may not be identical to their

extant relatives, more information regarding the origin and evolution of this significant tropical family may become clearer.

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CHAPTER 12

WHENCE THE FLORA OF SOUTHERN SOUTH AMERICA? BIASES MAY DISTORT OUR CONCLUSIONS

*Beryl B. Simpson**

ABSTRACT

There is little doubt that the flora of southern South America is unique, whether one considers the Chilean Matorral, the Patagonian steppes, or the temperate rainforests. In fact, the flora of southern South America is so different from that of the tropical regions to the north that South America has been called a hybrid continent, with the suggestion that it consists of a tropical land mass and an austral fragment, each carrying a distinctive flora, that rafted to their present positions and sutured together to form the current South American continent. Yet, there is no geological evidence for this notion, so the distinctiveness of the flora must be attributed to other factors—migration, dispersal, geological history, ecology, or a combination of all four. Attempts to explain the origins of South America's southern flora have tended to focus on "source areas," whether from Gondwana, the Neotropics, or the temperate areas of the Northern Hemisphere. In this review, I use this same approach but do so by assessing 106 molecular phylogenies of plant genera with species in southern South America, in order to see what they indicate about the origins of the flora. After evaluating the studies, I conclude that, to date, they say as much about the interests of the researchers as about the development of the flora. I suggest, instead, that many of the dominant elements of this unique flora are primarily the result of evolution of autochthonous taxa in response to changing geology and climatic factors across the Tertiary and Quaternary. Over this period of 65 million years, southern South America became progressively ecologically different from tropical South America, leading to selection and diversification of native elements in increasingly cool conditions while simultaneously fostering colonization by elements from temperate regions elsewhere.

Key words: amphitropical, Gondwana, Patagonia, southern South America.

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The flora of southern South America, defined here as the area south of the Tropic of Capricorn (in this paper basically the parts of the Cono Sur, or Southern Cone, inhabited by temperate vegetation) has fascinated botanists at least since the time of Hooker (1844, 1867). This interest stems from the unique aspects of the vegetation that include the southern rainforests, the wind swept steppes of Patagonia, and austral alpine areas, all of which differ in aspect and taxonomic composition from regions in South America north of the tropic. However, fascination with this part of South America also stems from physiognomic, and in many cases taxonomic, similarities to widely disjunct areas, such as the mountains of New Zealand and Australia, the chaparral of western North America, and the warm deserts of North America. The rest of South America has its own comparatively unique floras—the Neotropical rainforests, Tropical Andes, the dry Cerrado, and the Caatinga. It is this striking distinction between northern and southern parts of the continent that has led to South America being labeled a "hybrid" continent (Humphries & Parenti, 1986; Crisci et al., 1991). Yet, geology tells us that within the timeframe of the diversification of modern flowering plants, South America has been a single continent (Ramos, 2008), so the flora must have arisen in situ. In developing this idea, I point out the modern diverse and distinctive vegetation types in southern South America and briefly review the geological and climatological changes that occurred from the Late Cretaceous to the end of the Pleistocene that were influential in determining their modern physiognomies and taxonomic composition. As a potential aid in showing sources of current floristic elements, I summarize molecular phylogenetic studies of genera occurring in southern South America and provide examples that show the myriad ways in which plants arrived and/or diversified in this region. However, I also emphasize that this approach provides a biased sample and thus does not fully represent the complex origins of southern South American flora.

OVERVIEW OF THE FLORA AND HISTORICAL GEOLOGY OF SOUTHERN SOUTH AMERICA

VEGETATION OF SOUTHERN SOUTH AMERICA

The general types of vegetation in southern South America south of 30°S are forest, various kinds of scrub, grasslands, and desert. The forests of southern Chile have been the focus of many biogeographical studies (Arroyo et al., 1996). These forests range from north to south across 17.5° of latitude and from sea level to 2000 m elevation but are currently isolated by 1500–2000 km from other forests in South America (Arroyo et al., 1996). Wet conditions favorable for forests are caused by westerly winds that come in from the Pacific and then hit the southern Andes, dropping their moisture as they rise. In the extreme southern part of the continent, the forest gives way to Magellanic moorland (Arroyo et al., 1996). The forests have been divided into the boreal temperate evergreen or Magellanic rainforest in the south, the perhumid temperate rainforest (often divided into Valdivian and north Patagonian rainforests) farther north, and finally, north of Chiloé Island, the seasonal or deciduous forest. While difficult to show on a flat map, these types of vegetation often replace one another altitudinally rather than strictly latitudinally. Various species of *Nothofagus* Blume (Nothofagaceae) dominate these forests, but others belonging to *Austrocedrus* Florin & Boutelje, *Fitzroya* Hook. f. ex Lindl. (both Cupressaceae), *Gaultheria* L. (Ericaceae), *Laurelia* Juss. (Atherospermataceae), and *Maytenus* Molina (Celastraceae) are also common. Arroyo et al. (1996) thoroughly summarized the history of the South American temperate forests and concluded that 25% of the woody genera are of austral (Gondwanan) origin, slightly

less than one quarter have Neotropical forest affinities, and one third of the woody genera are endemic to this region (including neighboring Argentina and the Mediterranean shrublands to the north), with 80% of these being monotypic. They also pointed out that the southern forests have much higher species richness than the temperate rainforests of the U.S. Pacific Northwest and adjacent British Columbia, which is almost double in size.

Despite the emphasis on the forested regions of Chile, the majority of southern South America is covered by open vegetation types dominated by shrubs, herbs, and grasses. The Alto Andean vegetation covers the upper elevations of the southern Andes from ca. 30°S to Tierra del Fuego. As latitude increases, the height of this band of vegetation decreases from ca. 4000 m in the north (ca. 25°) to 500 m in the far south. The aspect of this vegetation is "alpine-like," with grasses and forbs, the last often mat-forming. Grasses, legumes, and composites are the most species-rich families.

Most of central Chile, from 29°S to 38°S, is considered the Mediterranean zone, grading irregularly into forest in the south and desert in the north. The form of its vegetation varies from grass steppe (at high elevations) to spiny thickets to palm forest. The climate is influenced by the cold, coastal Humboldt ocean current that leads to dry summers and mild, wetter winters. Within this region there are occurrences of *Nothofagus* that straggled in from the south (or, in some cases, remained behind as glaciers retreated at the end of the Pleistocene), fog forests on the western side of the coastal range, and remains of sclerophyllous forest that are now mostly replaced by stands of *Vachellia caven* (Molina) Seigler & Ebinger (formerly *Acacia caven* Molina) and *Prosopis* L. (both Fabaceae). The "true" Mediterranean-type vegetation is the Matorral, consisting of arid-adapted shrubs such as *Puya* Molina (Bromeliaceae), *Flourensia* DC., and *Baccharis* L. (both Asteraceae). The Matorral has been well studied in terms of its phytogeographic relationships because of its physiognomic resemblance to the chaparral of California. Indeed the Matorral has been shown to share, due to recent human introductions, many species with the chaparral of southern California (cf. Mooney, 1977). Yet, about 10% of the native genera and 95% of the species are endemic (Rundel, 1981).

Across the Andes in Argentina, there is the spillover of forest from Chile on the eastern side of the Andes that gives way to the large expanse of the Patagonian plateau, primarily semidesert but with a large component of shrubland and grass steppe. In the driest areas there is a preponderance of Chenopodiaceae, whereas dwarf and cushion shrubs, mostly Asteraceae, predominate in the semidesert habitats. The shrub steppe has comparatively larger plants consisting of species of *Adesmia* DC. (Fabaceae), *Berberis* L. (Berberidaceae), *Chuquiraga* Juss. (Asteraceae), *Lycium* L. (Solanaceae), *Mulinum* Pers. (Apiaceae), and *Schinus* L. (Anacardiaceae). In scattered wet areas, sedges are abundant.

North of the steppe is the expansive Monte Desert with *Larrea cuneifolia* Cav. (Zygophyllaceae), *Acacia* Mill. spp., *Prosopis* spp. (both Fabaceae), and a variety of cacti. There has been extensive work on this region because many of the dominant genera are shared with the deserts of North America (cf. Orians & Solbrig, 1977).

To the east of the Monte Desert, the Espinal, another dense scrub, dips below the 30th parallel but is mostly a tropical formation. Finally, easternmost are the grasslands and pampas that figure prominently in the economy of Argentina and are the most extensive vegetation type of Uruguay.

GEOLOGICAL AND CLIMATOLOGICAL CHANGES OF SOUTHERN SOUTH AMERICA SINCE THE LATE CRETACEOUS

Since the Cretaceous, southern South America has undergone profound changes in land surface area, topology, and climate (Ortiz-Jaureguizar & Cladera, 2006). In the Early Cretaceous (170 Ma),

the southern continents were united as Gondwana. There was less exposed land area in what is now southern South America than at present, and the landscape was comparatively flat. Dominant plants included gingko, conifers, ferns, and some early angiosperms. There appear to have been communities of forest, woodlands, aquatics, and "grasslands," with a seasonable climate constantly affected by volcanism (Cuneo, 2003). At ca. 125 Ma, Africa split from Gondwana and at ca. 80 Ma, New Zealand separated from the southern land mass. In the Albian (112–99 Ma), fossils from Antarctica show the presence of *Podocarpus* L'Hér. ex Pers. (Podocarpaceae), Myrtaceae, Proteaceae, Sapindaceae, and *Gunnera* L. (Gunneraceae) (Cuneo, 2003). By Maastrichtian times (70–65 Ma; Fig. 1) in Chubut, there were aquatic ferns, gymnosperms, and water lilies (*Nymphaea* L.) (Gandolfo, 2003). While no macrofossil remains of *Nothofagus* have been found in Patagonia to date, pollen of all three palynological groups of *Nothofagus* have been recovered (Romero, 1986). A Paleocene flora (ca. 61.6 Ma) from Patagonia has shown how diverse the flora of the region was with fossils of 36 angiosperm families, including Fabaceae, Lauraceae, Menispermaceae, Rosaceae, and Urticaceae, among others. The taxa present and leaf compressions indicate an average annual temperature of ca. 14°C and an annual precipitation of 115 cm, which is consistent with an absence of an Andean rain shadow at that time (Iglesias et al., 2007). From Late Paleocene/Early Eocene times (ca. 52 Ma), a very rich fossil flora (102 leaf species) has been uncovered at Laguna del Hunco in northern Chubut, with palms, cycads, *Araucaria* Juss. (Araucariaceae), *Podocarpus*, Proteaceae, *Myrica* L. (Myricaceae), Matorral-like elements, and some Australasian elements now extinct in South America (Wilf et al., 2003). The fossil flora suggests low elevation with a maritime influence and was, according to Wilf (2003), already diverse with a mosaic of vegetation types (Gandolfo et al., 2011). Romero (1986) likened the Paleocene flora of Gulfo San Jorge in eastern Argentina (44°S–47°S) to that of modern southern Brazil, with a mixture of mangroves, swamp forest, savannas, and tropical forest. At mid-southern latitudes, precipitation appeared to have been around 200 cm per year with a mean annual temperature of 25°C (Hinojosa, 2003). By mid-Eocene, there was a shift to a more temperate and drier climate that led to a mixture of tropical and warm temperate forest consisting of both New World tropical and austral elements (Hinojosa, 2003). At about the same time, Australia split from Antarctica. The cooling trend of this period culminated in the Late Eocene/Early Oligocene (33 Ma) with a significant drop in temperature to an annual average of 15°C and a reduction in precipitation to ca. 50 cm in places, resulting in a cool, temperate, comparatively dry flora with *Nothofagus*.

The Oligocene (28–34 Ma) was a time of climatic events that affected the climate and consequently the vegetation of southern South America. It was also the epoch during which (ca. 31 Ma) there is the earliest evidence of Antarctic glaciation (Chinn, 1996). More or less simultaneously (30 Ma), the Drake Passage opened with a movement of South America away from the Antarctic Peninsula. This event severed any direct connection among the former austral landmasses and altered the flow of southern Pacific Ocean currents. Anderson et al. (2011) also emphasized the progressive cooling of Antarctica during the Cenozoic with a diverse flora in the Eocene, a mosaic of *Nothofagus* and conifer-dominated woodlands during the Oligocene (34–23 Ma), and even localized pockets of tundra lasting until the Miocene, but they suggested that there may have been connections ranging from continuous to tenuous between South America and Australasia across western Antarctica, perhaps as late as 12.8 Ma.

In the Late Oligocene the initial phase of the uplift of the southern Andes occurred, but it was during the Miocene (7–28 Ma) that a series of major events were initiated that profoundly influenced the biota of southern South America. First,

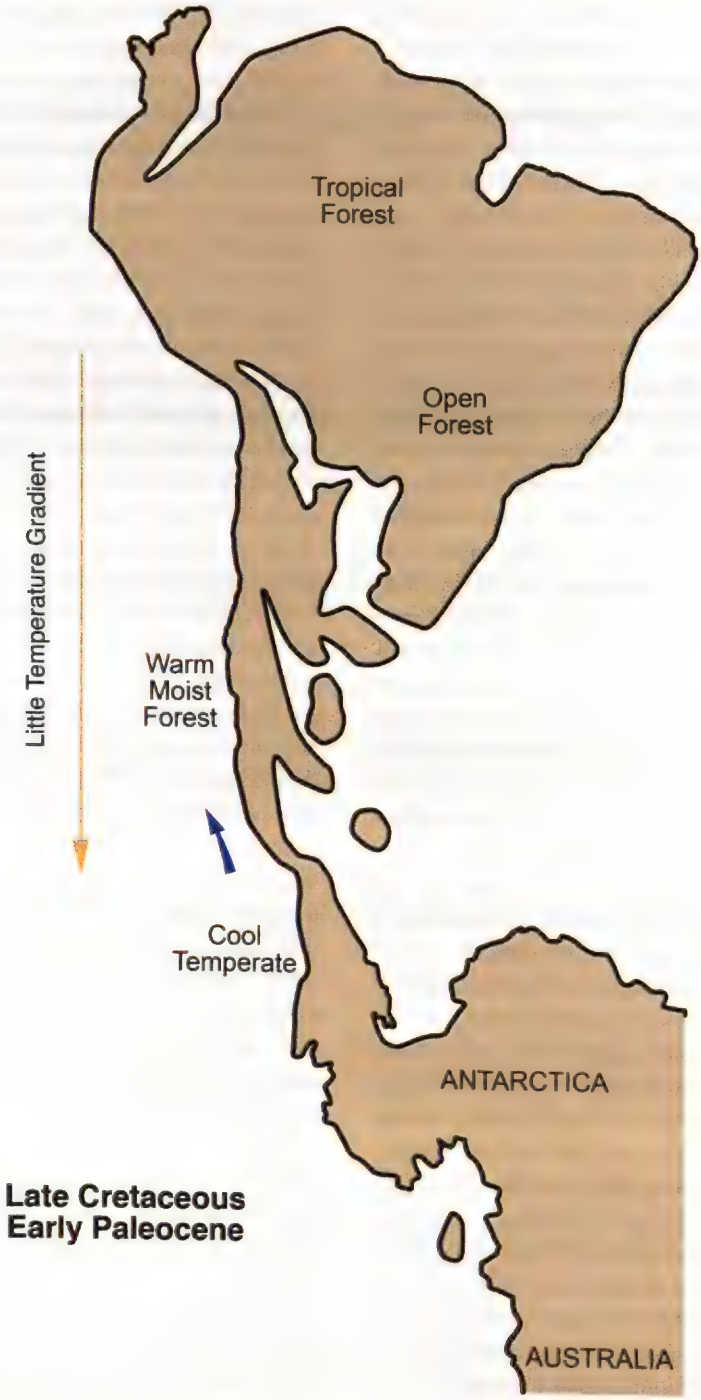

FIGURE 1. The configuration of South America in the Late Cretaceous, showing possible connections across western Antarctica to Australasia (modified from Pascual et al., 1996 and Iglesias et al., 2011, fig. 1D).

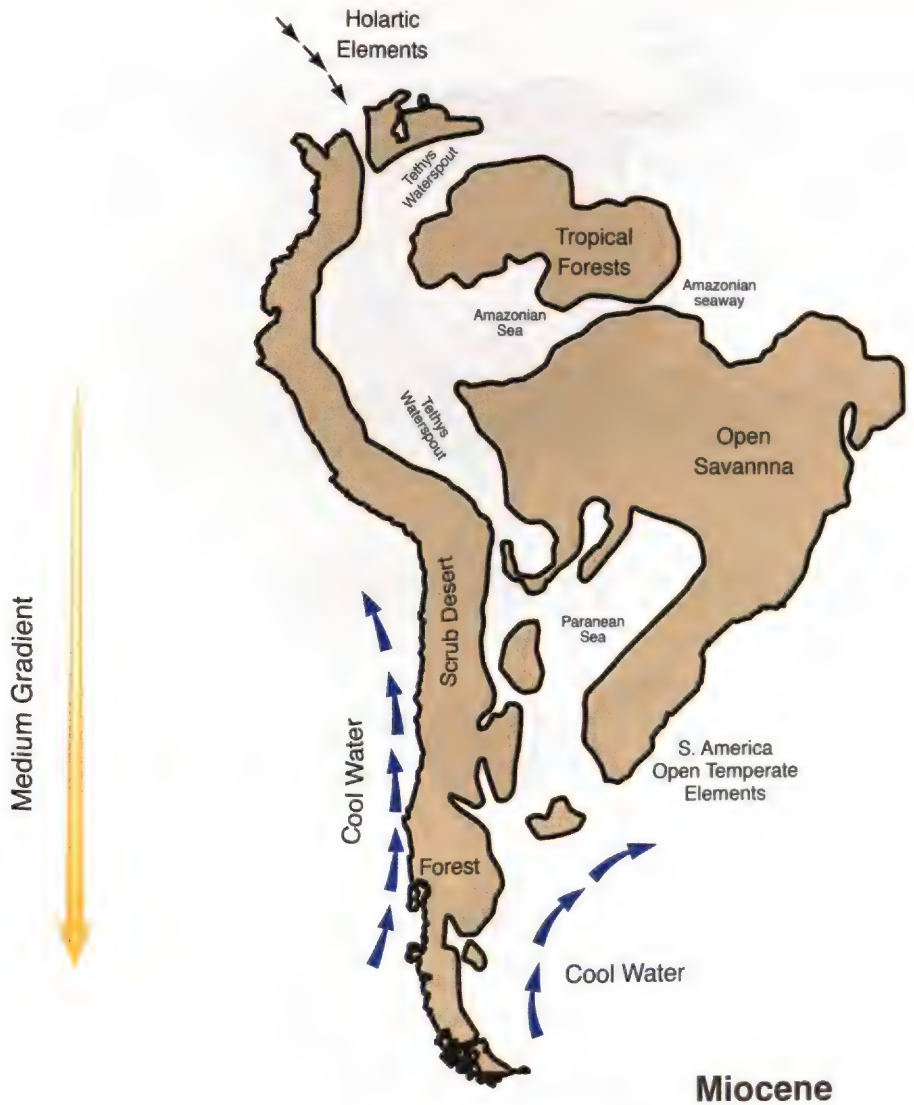

FIGURE 2. The configuration of positive land masses of South America during the Miocene, showing the inferred extent of sea incursions (modified from Donato et al., 2003).

during this epoch, much of South America was inundated by sea incursions (Fig. 2), undoubtedly fragmenting the distribution of many taxa. Between 16 and 17.5 Ma, the seas withdrew and the Andes began to rise significantly, as the Nazca plate impinged on the South American plate. The main uplift phase occurred between 15 and 9 Ma, with uplift culminating only about 1.2 Ma, with the most rapid rate of uplift occurring between 7 and 2 Ma. While the opening of the Drake Passage intensified the cooling of southern South America by setting in motion the circum-Antarctic

FIGURE 3. The configuration of South America during the Pliocene, when the modern topography and ocean currents had developed. ITCZ refers to the intertropical convergence zone.

current that reduced the mixing of polar and tropical ocean water, the uplift of the Andes, because of their height, created new, cold, alpine-like habitats. The newly created mountains also produced a rain shadow that drastically reduced the annual precipitation east of the Andes. As the Tertiary moved from the Miocene to the Pliocene, the Matorral, the Patagonian steppe, the Monte, and the eastern grasslands progressively assumed their modern form (Fig. 3).

Glaciations in southernmost South America have occurred since the Late Miocene as evidenced by scattered tills (Singer et al., 2004). The extent of glaciation was related to both the amount of moisture available for solidifying into ice and the amount of land above snow line. On

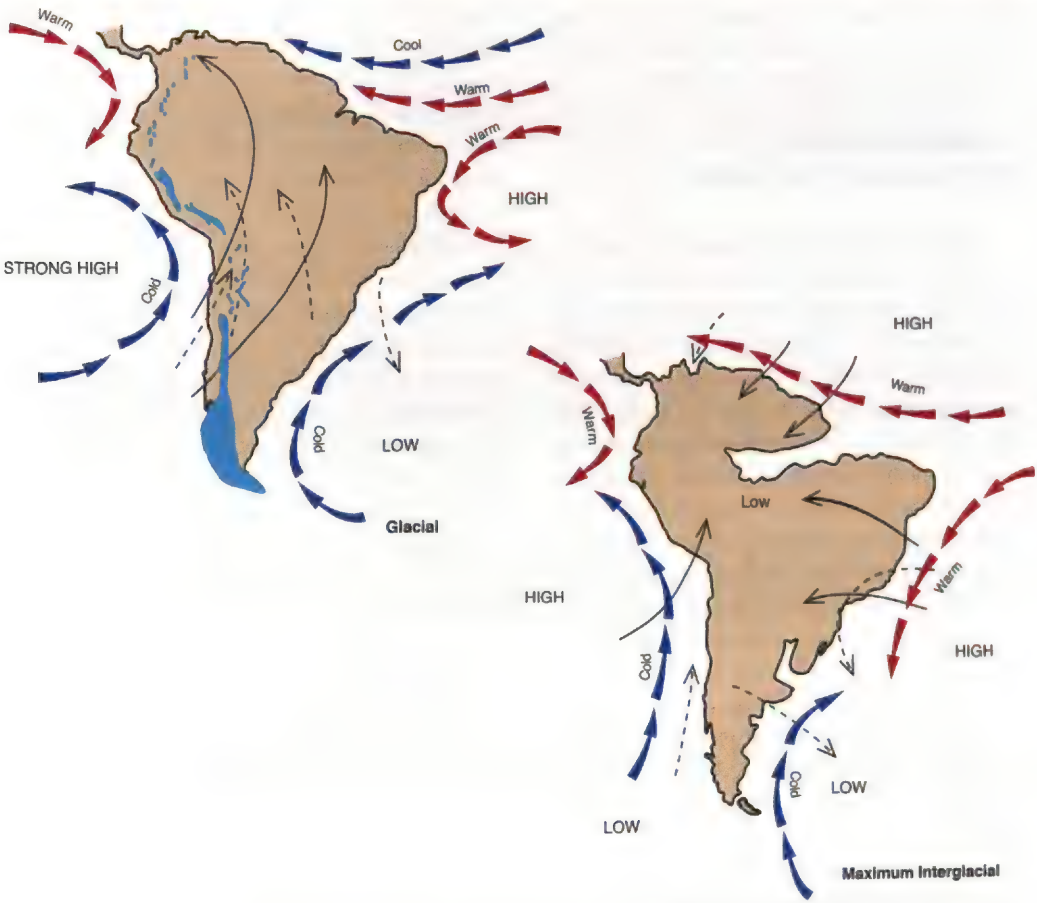

FIGURE 4. The configurations of South America during the Pleistocene. The proposed extent of ice and land surface area of South America during a major glacial event when ice would have completely covered all of the land surface of Chile south of 43°S (upper figure) and a maximum interglacial period with reduced land area due to sea level rise (lower figure).

the western side of the Andes, six glacial advances have been documented for the period between 33 and 15 ka (Lowell et al., 1995). Other glaciations undoubtedly occurred, but traces of them have been destroyed or the remains are so weathered that they cannot be dated. During the major Pleistocene glacial advances, ice covered all of the land west of the Andes south of 43°S (Clapperton, 1993; Fig. 4) and would have obliterated all of the vegetation in this area, except perhaps for a few refugial areas. Singer et al. (2004) provided a detailed account of glacial advances on the eastern side of the Andes at about 41°S, near Lago Llanquihue. Their work indicated that the Andes at this latitude were high enough to support mountaintop glaciers by 5 Ma, and they found evidence for 19 glacial advances. The glacial advance with the greatest eastward extent occurred between 1168 and 1016 ka. This advance is believed to have coincided with the maximum uplift of the southern Andes at 1.2 Ma (Singer et al., 2004). The last glacial maximum apparently

occurred 23 ka with deglaciation after 16 ka, more or less synchronously with the last advance in North America (Kaplan et al., 2004).

COMPILATION OF PHYLOGENETIC STUDIES

Many studies have tried to assess the origins of a flora by calculating taxonomic similarities between an area of interest and various other areas. A source area for shared taxa was usually considered to be the area with the largest number of species (when working at the generic level). While lists of shared genera or species between regions can give an indication of similarity and by extrapolation shared histories of these floristic elements, they do not accurately provide data on the area of origin of the elements, whether vicariance or dispersal led to co-occurrence in separated regions, directions of dispersal, areas of diversification, or time estimates of origination or diversification. Consequently, I compiled data from our, and other, published molecular phylogenies of genera that occur in southern South America with the aim of determining the sources of the various floristic elements. For a study to be used for this analysis, it had to include: a genus or subgeneric clade with (generally) more than one species in southern South America, a substantial number of the species of the genus, and a molecular phylogeny. Only gymnosperms and flowering plants are included. I classified the genera included into patterns that reflected the current distribution of their species: *austral*, genera with species that occur on two or more of the land masses that were formerly united into Gondwana; *amphitropical*, genera that occur in the temperate regions of the Northern and Southern Hemisphere and are not present in intervening tropical areas; *Neotropical*, taxa that occur primarily in the New World tropics; and *autochthonous*, groups that appear to have arisen and originally diversified in southern South America. The amphitropical category was divided into taxa that are disjunct between North and South America only, those that are amphitropical with congeners ranging widely across North America and temperate Eurasia (including the Mediterranean coast of Africa), and amphitropical genera with distributions that include North America, northern Eurasia, and Africa. For taxa placed into each of these categories, I noted what authors concluded from their phylogenetic reconstructions about the biogeographical history, or I provided my own interpretation from the phylogeny to determine which genera currently occur in southern South America because of vicariance, dispersal, or migration, or should be considered autochthonous. Where possible I tried to determine the direction of dispersal or migration and a timeframe for the initial occurrence of the species in southern South America.

RESULTS

Tables 1–6 list the 106 examples from studies that fulfilled the criteria above, and Table 7 summarizes the results of the compilation. This collection of studies is not exhaustive, and I apologize in advance to readers whose phylogenetic studies were not tabulated. To demonstrate some of these patterns, I discuss in detail selected examples, often from our laboratory.

AUSTRAL ELEMENTS

Similarities in aspect and shared important genera (*Nothofagus*, *Podocarpus*, etc.) between southern Chile and Australasia have prompted botanists since at least the middle of the 19th century (e.g., Hooker, 1844) to speculate about the historical link between the floras of those two, now widely separated, areas. As would be expected, groups shared between southern South America and New Zealand or Australia were early subjects of molecular phylogenies and constitute the second largest group of molecular studies included here (with the combined amphitropical group being larger). The interest in these austral elements stemmed from debates as to whether

TABLE 1. Genera with temperate austral distributions.

Genus (family) (no. of species)	Authors	Origin, direction[1]	Date[2]
Luzuriaga Ruiz & Pav. (Alstroemeriaceae) (3)	Chacón et al., 2012	SA > NZ	> 7 Ma
Nitrophila (Moq.) S. Watson/*Hemichroa* R. Br. (Amaranthaceae) (6–13/3)	Masson & Kadereit, 2013	Gondwana	19 Ma
Apium L. (Apiaceae) (25)	Spalik et al., 2010	(Eur) > SA > NZ	6.3 to SA
Chaerophyllum L. (Apiaceae) (33)	Spalik et al., 2010	(Eur) > Aus/NZ > sSA	2.8 Ma
Daucus L. (Apiaceae) (22)	Spalik et al., 2010	(Eur/Af) > SA > Aus	2.6 Ma
Lilaeopsis Greene (Apiaceae) (14)	Spalik et al., 2010	(NA) > SA > NZ	>27 Ma
Schizeilema (Hook. f.) Domin (Apiaceae) (1)	Nicolas & Plunkett, 2012	SA > NZ/Aus	—
Pseudopanax K. Koch (Araliaceae) (12–15)	Mitchell & Wagstaff, 2000	Gondwana	Old
Araucaria Juss. (Araucariaceae) (18)	Setoguchi et al., 1998	Gondwana	Cretaceous
Abrotanella Cass. (Asteraceae) (20)	Swenson & Bremer, 1997; Wagstaff et al., 2006	Gondwana	19–4.2 Ma
Leptinella Cass. (Asteraceae) (34)	Himmelreich et al., 2012	NZ > SA	13–10 Ma
Laurelia Juss./*Laureliopsis* Schodde (Atherospermataceae) (2)	Renner et al., 2000	SA > NZ	50–30 Ma
Myosotis L. (Boraginaceae) (100)	Winkworth et al., 2002	(NA) > Australasia > sSA	post-Pliocene
Cardamine L. (Brassicaceae) (200)	Bleeker et al., 2002	SA > Australasia	> 500,000 yr BP
Jovellana Ruiz & Pav. (Calceolariaceae) (4)	Nylinder et al., 2012	sSA > NZ	ca. 9 Ma
Coriaria L. (Coriariaceae) (5+)	Yokoyama et al., 2000	NZ > sSA	Cenozoic
Caldcluvia D. Don (Cunoniaceae) (11)	Bradford & Barnes, 2001	Gondwana	—
Eucryphia Cav. (Cunoniaceae) (6)	Bradford & Barnes, 2001	Gondwana	—
Fitzroya Hook. f. ex Lindl./*Diselma* Hook. f. (Cupressaceae) (1/1)	Yang et al., 2012	Gondwana	52–35 Ma
Carpha Banks & Sol. ex R. Br. (Cyperaceae) (13–15)	Zhang et al., 2004	Australasia > sSA	recent
Oreobolus R. Br. (Cyperaceae) (14)	Chacón et al., 2006	Aus > sSA	> 4 Ma
Aristotelia L'Hér. (Elaeocarpaceae) (5)	Bradford & Barnes, 2001; Crayn et al., 2006	Aus/NZ < ? > SA; equivocal	> 25 Ma
Sophora L. sect. *Edwardsia* (Salisb.) Seem. (Fabaceae) (17)	Hurr et al., 1999	NZ > SA	5–2 Ma
Gentianella Moench (Gentianaceae) (200)	von Hagen & Kadereit, 2001	(Asia > NA) > SA > NZ	3 Ma
Gunnera L. (Gunneraceae) (30–40)	Wanntorp & Wanntorp, 2003	Gondwana	Cretaceous
Nothofagus Blume (Nothofagaceae) (34)	Manos, 1997; Knapp et al., 2005	Gondwana	70–25 Ma
Hebe Comm. ex Juss. (Plantaginaceae) (120)	Wagstaff et al., 2002	NZ > SA	> 25 Ma

(continued)

TABLE 1. *(continued)*

Genus (family) (no. of species)	Authors	Origin, direction[1]	Date[2]
Ourisia Comm. ex Juss. (Plantaginaceae) (28)	Meudt & Simpson, 2006	SA > NZ/Tas	Pliocene?
Lepidothamnus fonkii Phil./*Lepidothamnus laxifolius* (Hook. f.) Quinn (Podocarpaceae) (2)	Biffin et al., 2010	Gondwana	Cretaceous
Podocarpus smithii de Laub./*Podocarpus salignus* D. Don (Podocarpaceae) (94)	Biffin et al., 2010	AUS > sSA	Pliocene
Muehlenbeckia Meisn. (Polygonaceae) (23)	Schuster et al., 2011	AUS > SA	—
Alloxylon P. H. Weston & Crisp/*Telopea* R. Br./*Embothrium* J. R. Forst. & G. Forst. (Proteaceae) (4/5/8)	Barker et al., 2007	Gondwana	50 Ma
Gevuina Molina/*Cardwellia* F. Muell. (Proteaceae) (1/1)	Barker et al., 2007	Gondwana	48 Ma
Orites R. Br./*Neorites* L. S. Sm. (Proteaceae) (7/1)	Barker et al., 2007	Gondwana	45 Ma
Panopsis Salisb. ex Knight/*Brabejum* L. (Proteaceae) (11/1)	Barker et al., 2007	dispersal equivocal	40 Ma
Anemone L. (Ranunculaceae) (150)	Meyer et al., 2010	(NA) > SA > Aus/NZ	Tertiary
Caltha L. (Ranunculaceae) (12)	Schuettpelz & Hoot, 2004	(NA) > SA > NZ	Tertiary
Discaria Hook. (Rhamnaceae) (6–8)	Aagesen et al., 2005	Australasia > SA?	probably recent
Forstera L. f./*Phyllachne* J. R. Forst. & G. Forst. (Stylidiaceae) (5)	Wagstaff & Wege, 2002	Australasia > sSA	6 Ma
Tetrachondra Petrie ex Oliv. (Tetrachondraceae) (2)	Wagstaff et al., 2000	SA > NZ	ca. 2.5 Ma
Drimys J. R. Forst. & G. Forst./*Pseudowintera* Dandy/*Zygogynum* Baill. (Winteraceae) (6/3/50)	Marquínez et al., 2009	Gondwana	84–69 Ma

[1] The following abbreviations and symbols are used in Tables 1–7: The symbol > indicates the direction of migration (*from* > *to*); Af = Africa; Aus = Australia; c = central; Eur = Europe; N = North; NA = North America; nSA = northern South America; n temp = north temperate; NZ = New Zealand; OW = Old World, unspecified; S = South; s = southern; SA = South America; sSA = southern South America; Tas = Tasmania; temp = temperate. A locality in parentheses indicates that the initial dispersal was from the area in parentheses to the area from which dispersal went to South America.

[2] Ma = millions of years ago; yr BP = years before present.

shared taxa are due to vicariance of continuous distributions from Australasia across Antarctica to South America or from long-distance dispersal. Table 1 lists the studies included here. Of the 41 studies dealing with austral taxa, I was able to determine the directions of dispersal or vicariance for 39. Of the 39, 14 (36%) were considered to be the result of Gondwanan vicariance, 13 (33%) appear to have dispersed via long-distance dispersal from South America to Australasia, and 12 (31%) seem to have dispersed from Australasia to southern South America. *Caltha* L., originally considered to show a Gondwanan pattern (Schuettpelz & Hoot, 2004), is now considered to be the result of long-distance dispersal (Spalik et al., 2010). For distributions deemed to have resulted from long-distance dispersal, time estimates range from 50 Ma to 500 ka (Table 1).

An example of an austral pattern is shown by *Ourisia* Comm. ex Juss. (Plantaginaceae, Fig. 5), a genus of 28 suffruticose or herbaceous perennial species (38 taxa), with 15 occurring in South America from Venezuela to southern Chile (10 of the 15 species occur south of 33°S), 12 species in New Zealand, and one species in Tasmania (Meudt & Simpson, 2006). Species in both South America and in Australasia grow in wet-rock, high-elevation habitats. Like many taxa with an austral distribution, a relevant question is, when and how did the South American–New Zealand pattern arise? Our molecular phylogenetic analysis of *Ourisia* clearly showed that the genus arose in South America and dispersed to Australasia (Fig. 5). While not dated, the phylogeny suggests at least a mid-Cenozoic dispersal, since the basal species are from central Chile. The genus also exhibits a within–South America pattern that may prove relatively common in Andean taxa, namely, a probable ancestral distribution in south-central western South America and a subsequent spread northward and southward along the Andes.

Clearly, patterns are complex, with some species-rich groups like *Ourisia* native to South America and others like *Hebe* Comm. ex Juss. native to New Zealand (Table 1); occurrences in both areas are the result of long-distance dispersals at various times in the Cenozoic. In fact, of the austral genera surveyed, 66% (20 of the 30 studies with time estimates) have disjunct patterns that are considered to be the result of dispersal within the last 27 million years.

NORTH TEMPERATE–SOUTH TEMPERATE AMPHITROPICAL GROUPS

As in the case of the austral pattern, botanists have been fascinated for more than a hundred years by taxa that occur disjunctly in the Northern and Southern hemispheres (Gray & Hooker, 1880; Bray, 1898, 1900), particularly between North and South America.

Tables 2–4 summarize the phylogenetic studies regarding genera that exhibit a temperate Northern Hemisphere to southern South America disjunct distribution pattern. Many of these are amphitropical groups discussed in Raven's classic paper (1963) on New World plant disjunction that have subsequently been investigated using phylogenetic methods to determine the direction, and to some extent timing, of their disjunctions. I have purposely excluded several studies of genera (many included in Raven's 1963 analysis) in which a single species (or species pair) is disjunct, even if that genus has a molecular phylogeny.

Of the 106 phylogenetic studies included here, 12 (11%) show a North America–South America (only) disjunct pattern (Table 2). Of these 12, nine (75%) are interpreted to be the result of dispersal from North to South America and only three (25%) from South America to North America. The four independent dispersals of *Hoffmannseggia* Cav. from South America (Simpson et al., 2004a, 2004b) to North America or the two independent dispersals of neo-*Astragalus* L. to South America (Scherson et al., 2008) are not counted independently. In the case of *Hoffmannseggia*, only one of the dispersal events was from southern South America (Fig. 6).

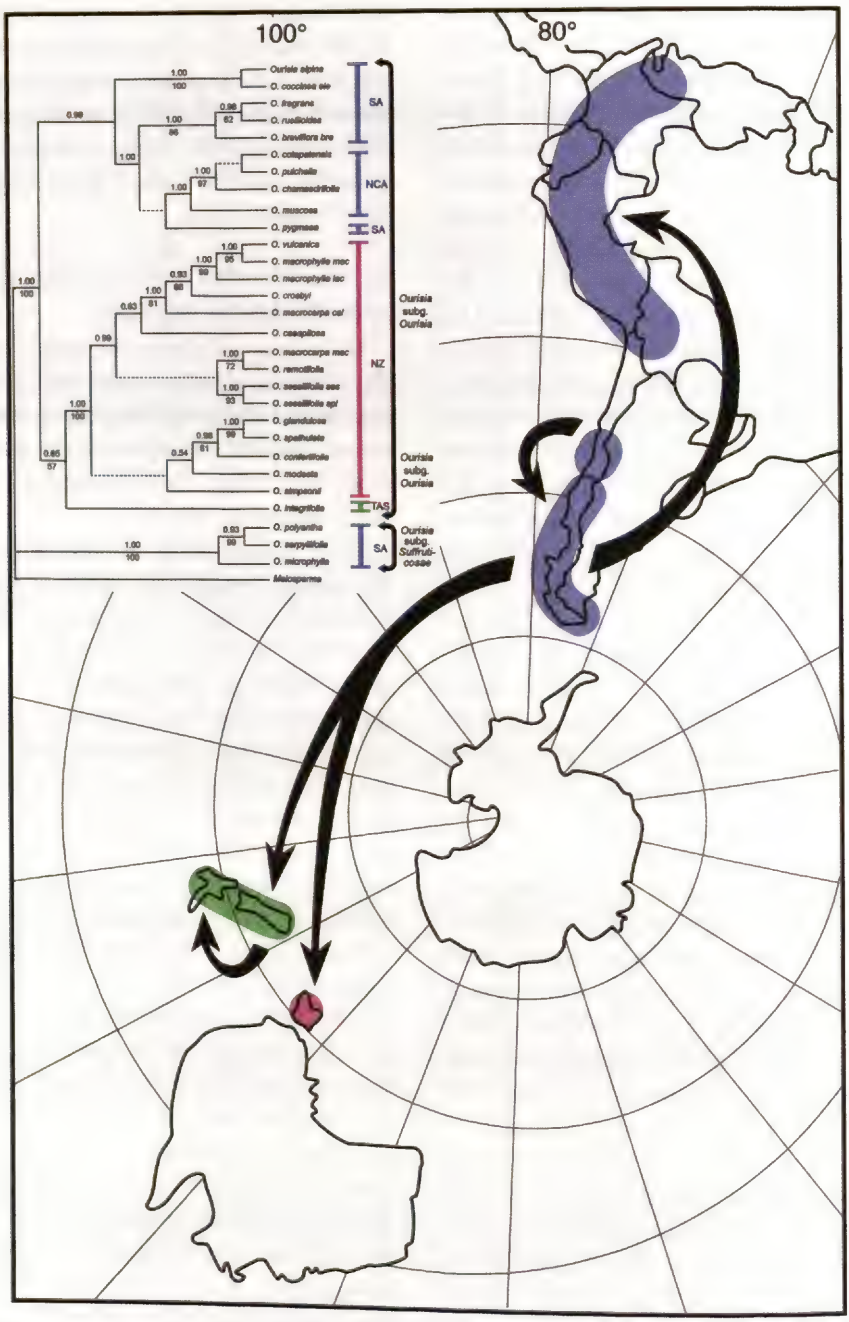

FIGURE 5. Phylogeny and biogeography of *Ourisia* (Plantaginaceae) with an austral pattern, showing the origin of the genus in southern South America, its spread north and south in the Andes, and its dispersal to New Zealand and Tasmania (redrawn from Meudt & Simpson, 2006). NCA = North Central Andes; NZ = New Zealand; SA = South America; TAS = Tasmania.

TABLE 2. Amphitropical genera distributed between temperate North and South America only. See the footnotes to Table 1 for a key to the abbreviations.

Genus (family) (no. of species)	Authors	Origin, direction	Date
Nitrophila (Moq.) S. Watson (Amaranthaceae) (5)	Masson & Kadereit, 2013	SA > NA	4.2 Ma
Grindelia Willd. (Asteraceae) (51–76)	Moore et al., 2012	probably NA > SA	—
Tiquilia Pers. subg. *Tiquilia* (Boraginaceae) (4)	Moore et al., 2006	NA > SA	post-Pleistocene
Astragalus L. (neo-*Astragalus* clades G & F, Fabaceae)	Scherson et al., 2008	NA > SA (2 times)	> 1.48 Ma
Hoffmannseggia Cav. (Fabaceae) (21)	Simpson et al., 2004b	SA > NA (4 times)	Miocene to Pleistocene
Festuca L. (Poaceae) (450)	Inda et al., 2008	NA > SA	3.8 Ma
Scleropogon Phil. (Poaceae) (1)	Peterson & Columbus, 1997	NA > SA	recent
Navarretia Ruiz & Pav. (Polemoniaceae) (30)	Morrell et al., 2000	NA > SA	recent
Gilia laciniata Ruiz & Pav. complex (Polemoniaceae) (6)	Morrell et al., 2000	NA > SA	> 3 Ma
Saxifragodes D. M. Moore (Saxifragaceae) (1)	Soltis et al., 2001	NA > SA	"old"
Plectritis (Lindl.) DC. (Valerianaceae) (5)	Bell & Donoghue, 2005	NA > SA	> 25–20 Ma
Larrea Cav. (Zygophyllaceae) (5)	Lia et al., 2001	SA > NA	8.4–4.2 Ma

TABLE 3. Amphitropical genera, widespread in north temperate regions and southern South America (not in sub-Saharan Africa). See the footnotes to Table 1 for a key to the abbreviations. Numbers in parentheses indicate previous or subsequent dispersals.

Genus (family) (no. of species)	Authors	Origin, direction	Date
Apium L. (Apiaceae) (25)	Spalik et al., 2010	Eur > SA > (NZ)	6.3 Ma to SA
Daucus L. (Apiaceae) (22)	Spalik et al., 2010	Eur > SA > (Aus)	2.6 Ma
Osmorhiza Raf. (Apiaceae)(10)	Wen et al., 2002	(Asia) > NA > SA	recent
Hypochaeris L. (Asteraceae) (15)	Samuel et al., 2003; Tremetsberger et al., 2005	Eurasia > sSA	1–0.25 Ma
Carex L. sect. *Spirostachyae* (Drejer) L. H. Bailey (Cyperaceae) (25)	Escudero et al., 2008	Eur > sSA	—
Empetrum L. (Empetraceae) (3)	Li et al., 2002; Popp et al., 2011	NA > SA	0.59–0.26 Ma
Euphrasia L. (Orobanchaceae) (170–350)	Gussarova et al., 2008	Eurasia > sSA	> 8 Ma
Littorella P. J. Bergius (Plantaginaceae) (3)	Hoggard et al., 2003	NA > SA	Pleistocene
Scleropogon Phil. (Poaceae) (1)	Peterson & Columbus, 1997	NA > SA	recent
Primula L. (Primulaceae) (400)	Guggisberg et al., 2009	NA > SA	—
Anemone L. (Ranunculaceae) (150)	Schuettpelz & Hoot, 2004; Spalik et al., 2010	NA > SA	8.3–3.6 Ma
Caltha L. (Ranunculaceae) (12)	Schuettpelz & Hoot, 2004; Spalik et al., 2010	NA > SA > (NZ)	8.3–3.6 Ma
Chrysosplenium L. (Saxifragaceae) (57)	Soltis et al., 2001	Asia > sSA	"old"
Saxifraga L./*Saxifragella* Engl. (Saxifragaceae) (440/1)	Soltis et al., 2001	NA > SA	—
Cascadia A. M. Johnson/*Saxifragodes* D. M. Moore (Saxifragaceae) (1/1)	Soltis et al., 2001	NA > SA	—

TABLE 4. Amphitropical genera widespread in north temperate areas (including Africa) and southern South America. See the footnotes to Table 1 for a key to the abbreviations.

Genus (family) (no. of species)	Authors	Origin, direction	Date
Draba L. (Brassicaceae) (350)	Koch & Al-Shehbaz, 2002	NA > SA	Pliocene–Pleistocene
Lepidium L. (Brassicaceae) (175)	Mummenhoff et al., 2001	NA > SA	Pliocene–Pleistocene
Rorippa Scop. (Brassicaceae) (60)	Bleeker et al., 2002	NA > SA	100,000 yr BP
Sanicula L. (Apiaceae) (38)	Vargas et al., 1998	NA > SA	2–1 Ma
Ephedra L. (Ephedraceae) (50 to 65)	Huang et al., 2005	(Eur) > NA > SA	recent
Gentianella Moench (Gentianaceae) (256)	von Hagen & Kadereit, 2001	(Asia) > NA > SA > (Aus/NZ)	3 Ma
Lathyrus L. (Fabaceae) (160)	Kenicer et al., 2005	Eurasia > SA	—
Chaboissaea E. Fourn. (Poaceae) (4)	Sykes & Christensen, 1977	(Eur) > NA > SA	recent
Festuca L. (Poaeae) (500)	Inda et al., 2008	(Asia) > NA > SA	3.8 Ma
Ranunculus L. (Ranunculaceae) (600)	Hörandl et al., 2005	OW > sSA	—
Rubus L. (Rosaceae) (250)	Alice & Campbell, 1999	n temp > sSA	—
Mimulus L. (Scrophulariaceae) (120)	Beardsley & Olmstead, 2002	NA > SA	recent
Grabowskia Schltdl./*Lycium* L. (Solanaceae) (4/80)	Miller, 2002	NA > SA	—
Lycium L. (Solanaceae) (80)	Fukuda et al., 2001	equivocal	< 29 Ma

Of the more widespread north temperate taxa (including the north coastal region of Africa), 15 of the 106 (14%) have amphitropical distributions in southern South America. Of these 15, six (40%) appear to have colonized southern South America directly from Europe and/or Asia, and nine (60%) dispersed to South America from North America. None colonized North America or Eurasia from South America.

Finally, there are phylogenetic studies of 14 (13%) of the 106 included genera (only 13 of which indicate direction of dispersal) that are widespread north temperate taxa with species also occurring in Africa (other than circum-Mediterranean Africa) and with disjunct species in southern South America. Ten of these 13 (77%) appear to have dispersed from North America to South America, three of 13 (23%) from Europe/Asia to southern South America, and none from southern South America to north temperate regions.

Thus there are a total of 41 genera (39% of the 106) studied that exhibit various amphitropical patterns. Below are totals (and percentages) for north temperate genera (40 with data) disjunctly distributed in southern South America as a result of long-distance dispersals in the following directions:

North America to South America—28 (70%)
Europe/Asia to southern South America—9 (22.5%)
South America to north temperate regions—3 (7.5%)

The oldest dates proposed for any of these disjunctions is 25–20 Ma (*Plectritis* (Lindl.) DC., Bell & Donoghue, 2005), with most dated as post-Pliocene or even "recent" (Tables 2–4).

A classic example of a strictly New World amphitropical group is the genus *Larrea* Cav. (Zygophyllaceae). *Larrea* is a genus of five shrub species, with four species covering large amounts of the Monte and Patagonian steppe. In the Monte, *L. cuneifolia* Cav. is the dominant plant on the desert flats and *L. divaricata* Cav. is common along streambeds. In North America, *L. tridentata* (Sessé & Moc. ex DC.) Coville is a dominant species on flat areas of the Chihuahuan, Sonoran,

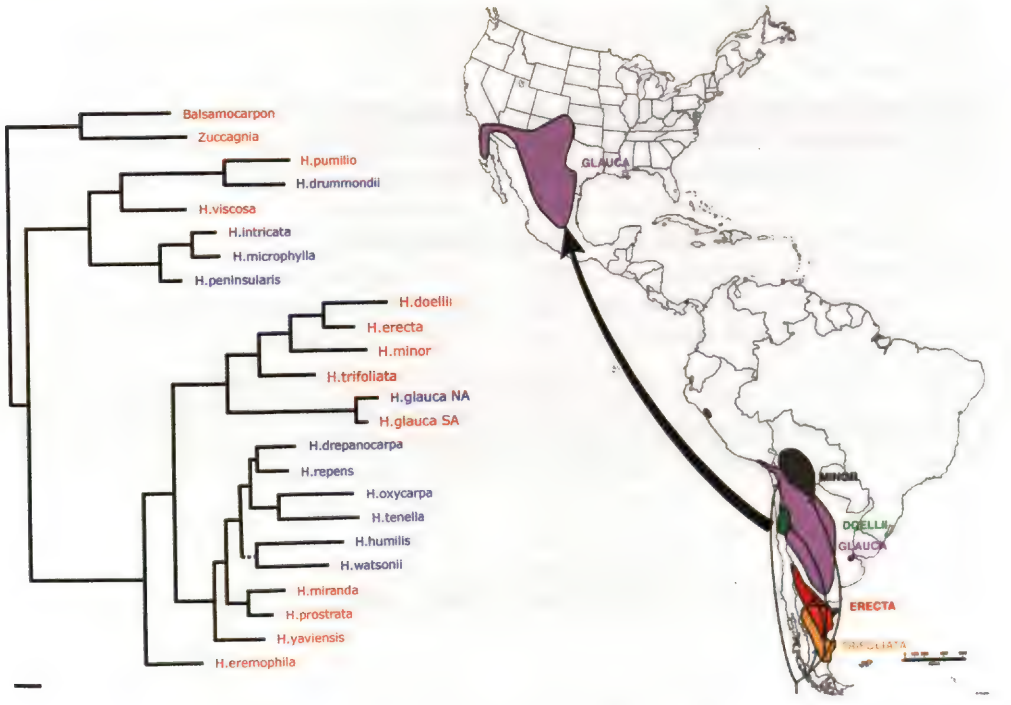

FIGURE 6. The phylogeny of *Hoffmannseggia* (Fabaceae), illustrating a New World amphitropical pattern with the dispersal of *H. glauca* from South America to North America (from fig. 2c in Simpson et al., 2004b). Names on the cladogram in red are South American species; those in blue occur in North America. This is one of the four dispersals from South America to North America leading to amphitropical patterns in the genus.

and Mojave deserts. There has been controversy over the years as to whether the genus arose in North or South America (reviewed in Hunziker et al., 1977), but a recent molecular study by Lia et al. (2001) showed conclusively that the genus is South American in origin, with a dispersal to North America occurring somewhere between 4.2 and 8.4 Ma.

The genus *Hoffmannseggia* (Fabaceae, Simpson et al., 2004a, 2004b) provides another example of a strictly New World genus that is amphitropical in distribution (Fig. 6). The genus has 21 species, 10 in North America and 10 in South America exclusively, with one species amphitropically distributed between the two continents. In North America, all species occur at relatively low elevations, whereas in South America, species occur from sea level to over 4000 m in the south Central Andes. An assessment of the biogeography in light of a well-resolved molecular phylogeny (Simpson et al., 2004a, 2004b) showed that the genus consists of five clades, four of which have taxa present in both North and South America. It is necessary to postulate at least four independent dispersals to North America to account for the North American members that are derived in each clade. While it was not possible to determine the timings of these dispersals, it was obvious from the phylogenetic analysis that they occurred at different times. Judging from the habitat preferences of the North American species, dispersals would probably have occurred within the last 15 million years.

NEOTROPICAL GROUPS

Eight studies listed in Table 5 (ca. 8% of the 106 included) are considered to show the presence of taxa in southern South America that are part of tropical groups that expanded their ranges into temperate regions by adapting to the cooler and drier conditions of southern South America during the Tertiary. While an Early Tertiary date was proposed for *Prosopis* (Bessega et al., 2006), most researchers consider the presence of these elements in southern South America to be post-Miocene (Table 5).

AUTOCHTHONOUS ELEMENTS

Sixteen genera (15% of the 106, Table 6) were classified autochthonous—taxa that arose in southern South America (or in a few cases west-central Chile) and diversified from there. This pattern consists of groups restricted to temperate South America or temperate South American genera that have radiated from this area with species reaching along the deserts of western South America, north along the Andes, into Patagonia, or even into southern Brazil (e.g., *Adesmia*, *Alstroemeria* L. [Alstroemeriaceae], *Calceolaria* L. [Calceolariaceae], *Nolana* L. f. [Solanaceae], and *Perezia* Lag. [Asteraceae]). The first molecular study to include a group originating in southern South America was that of Gengler-Nowak (2002, 2003) on *Malesherbia* Ruiz & Pav. (Malesherbiaceae). The genus consists of 12 species ranging from north-central Chile to the deserts of Peru. There is no doubt that the genus arose in South America, possibly in the Late Miocene or Early Pliocene, with most speciation attributable to Pleistocene glacial events.

Our work on *Perezia* (Simpson et al., 2009; Fig. 7) illustrates a group that arose in southern South America and expanded north along the Andes and eastward across the Patagonian plateau into southern Brazil. Despite the listing of *Perezia* as a "tropical group" by Moreira-Muñoz and Muñoz-Schick (2007), our phylogeny and the distribution of its outgroups indicate that the origin of *Perezia* was in temperate latitudes.

DISCUSSION

What do these studies tell us? What do they not tell us? First, they show that the flora of southern South America is derived from a number of sources, as has been well understood in the past. Second, if taken at face value (Table 7; Fig. 8) they indicate that more or less equal percentages of the flora are derived from north temperate groups, primarily groups that arose in and/or dis-

TABLE 5. Genera of tropical origin that have migrated into southern South America. See the footnotes to Table 1 for a key to the abbreviations.

Genus (family) (no. of species)	Authors	Origin, direction	Date
Diplolepis R. Br. (Apocynaceae) (11)	Hechem et al., 2011	tropics > S	post-Pliocene
Escallonia Mutis ex L. f. (Escalloniaceae) (69)	Zapata, 2013	tropics > S	post-Miocene
Heliotropium L. sect. *Platygyne* Benth. (Boraginaceae) (2)	Luebert et al., 2011b	tropics > sSA	post-Miocene
Heliotropium L. sect. *Plagiomeris* I. M. Johnst. (Boraginaceae) (3)	Luebert et al., 2011a, 2011b	tropics > sSA	post-Miocene
Prosopis L. (Fabaceae) (44)	Bessega et al., 2006; Catalano et al. 2008	tropics > N & S	> Early Tertiary
Pinguicula L. (Lentibulariaceae) (80)	Cieslak et al., 2005	tropics > temp sSA	—
Tarasa Phil. (Malvaceae) (30+)	Tate & Simpson, 2003	tropics > temp	—
Briza L. (Poaceae) (20)	Essi et al., 2008	Brazil > s Chile	—

TABLE 6. Autochthonous genera, with origins in southern South America. See the footnotes to Table 1 for a key to the abbreviations.

Genus (family) (no. of species)	Authors	Origin, direction	Date
Alstroemeria L. (Alstroemeriaceae) (50)	Chacón et al., 2012	sSA > tropics	crown 18 Ma
Azorella Lam. (Apiaceae) (26–28)	Nicolas & Plunkett, 2012	sSA > N and to higher elevations	—
Laretia Gillies & Hook. (Apiaceae) (2)	Nicolas & Plunkett, 2012	sSA > N and to higher elevations	—
Mulinum Pers. (Apiaceae) (20)	Nicolas & Plunkett, 2012	sSA	—
Pozoa Lag. (Apiaceae) (2)	López et al., 2012	in situ	recent split of 2 species
Nassauvia Comm. ex Juss. (Asteraceae) (38)	Maraner et al., 2012	sSA > N and up the Andes & E	—
Perezia Lag. (Asteraceae) (30-35)	Simpson et al., 2009	Chile > N & E	pre-Miocene onwards
Calceolaria L. (Calceolariaceae) (300)	Cosacov et al., 2009	sSA > N	Pliocene and later
Tristerix Mart. (Loranthaceae) (11)	Amico et al., 2007	c Chile > N & S	pre-Miocene
Malesherbia Ruiz & Pav. (Malesherbiaceae) (24)	Gengler-Nowak, 2002, 2003	c Chile	pre-Pliocene
Fuchsia L. (Onagraceae) (110)	Berry et al., 2004	possible sSA > nSA & se Brazil	ca. 26 Ma
Oxalis L. of Chile (Oxalidaceae) (480)	Heibl & Renner, 2012	c Chile > N & S	post-Miocene
Nolana L. f. (Solanaceae) (89)	Dillon et al., 2009	n Chile > N & S	15–10 Ma
Schizanthus Ruiz & Pav. (Solanaceae) (12)	Pérez et al., 2006	c Chile > N & S	Cretaceous onwards
Tropaeolum L. (Tropaeolaceae) (90)	Hershkovitz et al., 2006	c Chile > tropics	Early Cenozoic
Larrea Cav. (Zygophyllaceae) (5)	Lia et al., 2001	warm temp SA > S & W	8.4–4.2 Ma

persed from North America, and austral groups. Age estimates indicate that the North American temperate groups, and the few from Eurasia, arrived via long-distance dispersal in the later half of the Pliocene or more recently. For the taxa classified as austral, about 36% can be attributed to Gondwanan vicariance, about 33% appear to be native to South America and dispersed by long-distance dispersal to Australia/New Zealand, and 31% dispersed to southern South America from Australasia. Relationships with Africa are rare to nonexistent in the austral groups studied, presumably because Africa and South America split apart so much earlier than Australia/New Zealand/Antarctica, and the portions of Africa that remained closest to South America the longest were tropical areas. Finally, taking only these studies in account, they indicate that few elements arose and diversified in southern South America and that even fewer Neotropical groups were successfully able to move into, or persist in, southern South America as it became increasingly temperate during the Cenozoic.

Are we to take these percentages as a true reflection of the origins of the flora of southern South America? Certainly they are interesting in assessing particular patterns such as the New World amphitropical or austral distributions where specific questions about directions of dispersal and timings of colonization are of interest. Simply because of the interest in these questions, botanists have focused on groups exhibiting these relationships to the extent that they overshadow other patterns. Another reason for the apparent dominance of these patterns is the fact that fewer South American botanists than botanists in the U.S.A., Europe, and Australasia have been interested in investigating biogeographic questions using molecular phylogenetic methods. The seemingly important pattern of southern South American taxa with austral distributions as having come from (or gone to) New Zealand or Australia is un-

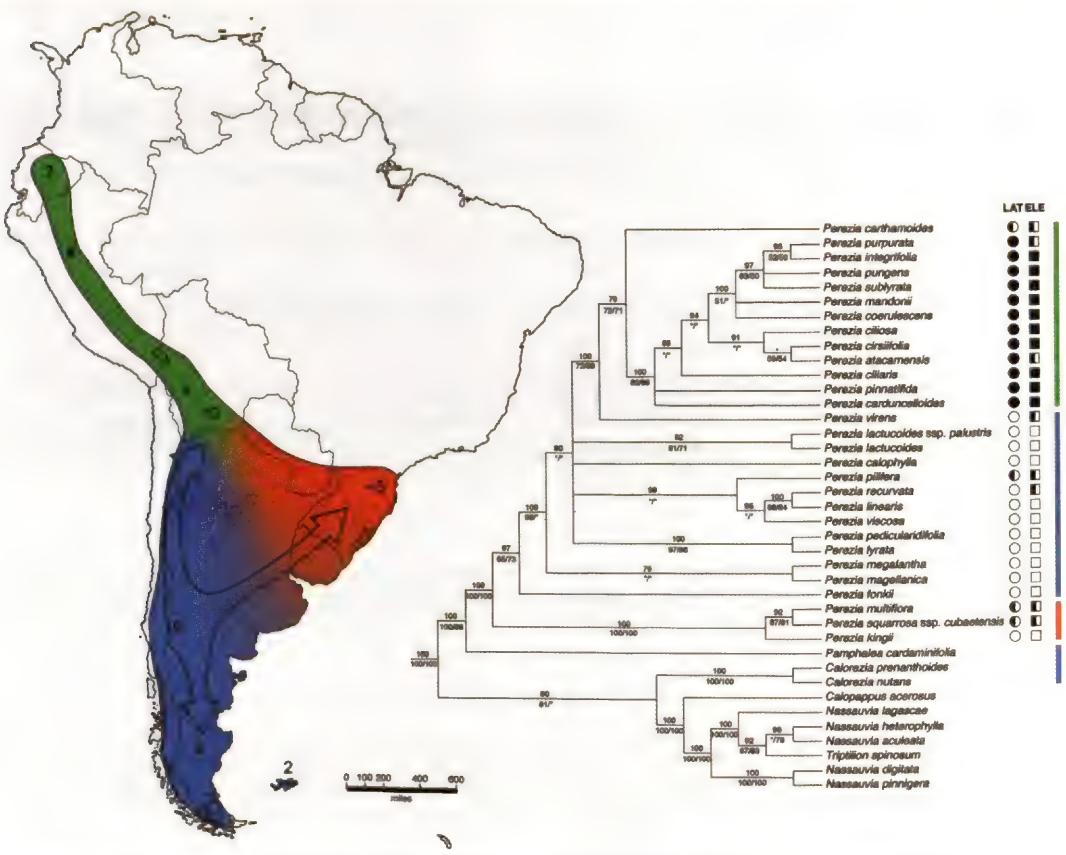

FIGURE 7. The distribution and phylogeny of *Perezia* (Asteraceae), an autochthonous genus showing the origin of the genus in southern South America and its proposed spread to southeastern Brazil and northward into the high tropical Andes (from Simpson et al., 2009). All of the outgroups are primarily temperate or subtropical in distribution. The circles indicate species distributions (black circle = north of 30°S latitude; white circle = south of 30°S). The squares represent the species altitudinal ranges (black square = above 2500 m; white square = below 2500 m. If a species range extends across these dividing points, the squares or circles are half shaded. The cladogram clearly shows that lower latitudes and higher elevations are derived in the genus.

doubtedly attributable to the taxa chosen to test whether Gondwanan vicariance or long-distance dispersal was the major factor in shaping the flora of New Zealand (or southern South America).

Several nonmolecular phylogenetic studies have also tried to assess the importance of austral connections for the southern South American flora. Arroyo et al. (1996) emphasized the high level of endemism (34%) of the southern rainforest woody genera (28 of 82 genera and one family they tabulated), but they also pointed out that 18 (22%) of these genera have southern, perhaps Gondwanan origins. Simpson and Todzia (1990), using plant data from the orophytic zone (alpine or supraforest zone) of Tierra del Fuego to calculate similarity values, concluded that 20% of the genera had austral relationships, a surprisingly similar percentage. However, neither study indicated directionality of the disjunctions nor had any direct dating. Looking from the other side of the world, Wardle et al. (2001) listed 40 species or species pairs of flowering plants that are shared between New Zealand and southern South America (of these only ca. 13 had molecular phyloge-

TABLE 7. Summary of biogeographic patterns, source areas, and postulated directions of dispersal based on 106 phylogenetic studies. See footnote 1 of Table 1 for a key to the abbreviations.

Pattern[1]/Direction[2]	No. of taxa	Percent of total taxa	No. of taxa in subgroup[3]	Percent of total taxa	Percent of subgroup taxa
Austral	**41**	**39%**			
SA > Aus/NZ			13	12%	32%
NZ/Aus > SA			12	11%	29%
Gondwana			14	13%	34%
Equivocal			2	2%	5%
Amphitropical	**41**	**39%**			
NA & SA only			12	11%	
NA > SA			9	8%	75%
SA > NA			3	3%	25%
NA/Eurasia & SA			15	14%	
NA > SA			9	8%	60%
Eurasia > SA			5	5%	33%
Asia > SA			1	1%	7%
NA/Eurasia/Africa & SA			14	13%	
NA > SA			10	9%	71%
Eurasia > SA			3	3%	21%
Equivocal			1	1%	7%
Neotropical	**8**	**8%**			
Tropics > sSA			8	8%	
Autochthonous	**16**	**15%**			
TOTAL TAXA	106	100%			

[1] Pattern refers to the geographical distribution of the genus.
[2] Direction refers to the postulated source area with the arrows > showing the direction of movement.
[3] Subgroup refers to both the different geographical patterns within the amphitropical group and the directional patterns within each pattern.

nies suitable for this study). From their data they concluded that Gondwanan connections played a greater role in the disjunctions of trees than for species of open habitats. Our compilation of molecular phylogenetic data would suggest that 39% of the genera of southern South America have a biogeographic relationship with Australasia, a figure higher than that suggested by nonmolecular studies. There are undoubtedly numerous other genera with austral distributions that do not have a molecular phylogeny. Renner et al. (2000) pointed out that there are many South American Asteraceae with South America–Australasian disjunctions (e.g., *Cotula* L., *Microseris* D. Don, *Centipeda* Lour., *Lagenophora* Cass., etc.) which lack molecular phylogenies, but whose distribution patterns must be due to long-distance dispersals because the origin of the Asteraceae postdates the breakup of Gondwana.

What do these studies say about vicariance versus dispersal? The very nature of modern molecular phylogenetic work necessitates using (for all practical purposes) modern species. Relationships "revealed" by these studies may often be skewed by the lack of knowledge of extinct species. We know, for example, that for *Nothofagus*, there are South American fossils of the "menziesi" pollen type (found in *Nothofagus* subg. *Lophozonia* (Turcz.) Krasser) from the Eocene to the Miocene, the "brasii" type (found in *Nothofagus* subg. *Brassospora*

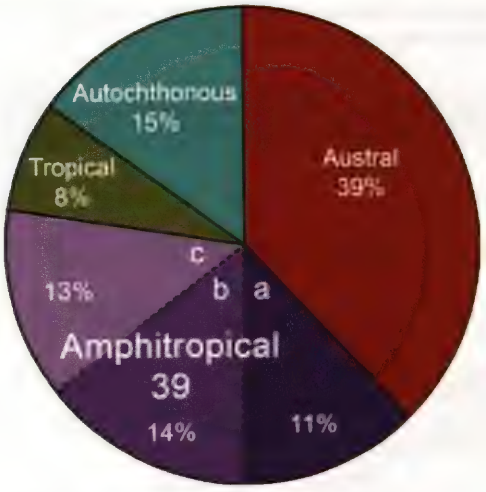

FIGURE 8. Percentages of the flora of southern South America originating from various sources as determined by molecular phylogenetic studies included in this article. *Amphitropical* = taxa that occur in southern South America and north temperate areas but not in Neotropical regions. Amphitropical subpattern a = amphitropical between North America/South America only; b = widespread north temperate taxa (excluding Africa, except for Mediterranean Africa) with amphitropical representatives in southern South America; c = widespread north temperate genera also occurring in Africa with amphitropical representatives in southern South America. The smaller numbers in each subpattern indicate the percentages of the total. *Austral* = genera that show connections with continents formerly united into Gondwana. *Autochthonous* = genera that appear to have arisen in southern South America. *Tropical* = Neotropical genera with species occurring in southern South America.

Philipson & M. N. Philipson) from the Eocene to the Miocene, and "fusca" pollen types (found in *Nothofagus* subg. *Nothofagus*) from the Oligocene to the Miocene (Palazzesi & Barreda, 2007). Today, only species of *Nothofagus* subg. *Lophozonia* and *Nothofagus* subg. *Fuscaspora* R. S. Hill & J. Read occur in southern South America and in Australia and New Zealand. Yet, Sanmartin et al. (2007) suggested that while the split between two of the subgenera, *Nothofagus* subg. *Nothofagus* and *Nothofagus* subg. *Brassospora*, can be explained by vicariance, the phylogeny of extant species of *Nothofagus* subg. *Lophozonia* and *Nothofagus* subg. *Fuscaspora* appears to be the result of long-distance dispersal from Australia because these are dated to be younger than any Gondwanan connection.

Other examples exist where fossil data can often present a very different picture from modern biogeography, as pointed out by Anderson et al. (2011), Mao et al. (2012), and Yang et al. (2012). For example, in his analysis of early Cenozoic conifers of Patagonia, Wilf (2012) pointed out that there are Paleocene fossils of *Acmopyle* Pilg. (Podocarpaceae), *Araucaria* sect. *Eutacta* Endl. (Araucariaceae), and *Papuacedrus* H. L. Li (Cupressaceae) from southern Australia and Patagonia, both of which were adjacent to Antarctica at this time. Today descendants of these groups are present only in Australasia. Likewise, the oldest unequivocal fossils of *Eucalyptus* L'Hér (Myrtaceae) are from the Eocene of the Laguna del Hunco Formation of Chubut, Argentina (Gandolfo et al., 2011). Today *Eucalyptus* occurs naturally only in the Old World, primarily Australasia. Perhaps the success of huge plantations of Australian *Eucalyptus* introduced into South America is the genus's way of reclaiming its ancestral home. On the other hand, fossils of *Austrocedrus* and *Fitzroya* (both Cupressaceae) have been found in Paleocene deposits of southeastern Australia, but today these genera are found only in South America. *Dacrycarpus* (Endl.) de Laub. (Podocarpaceae), today ranging in tropical montane areas from New Zealand to northern Burma, has abundant fossils in southeastern Australia and Patagonia (Wilf, 2012). Fossil evidence also clearly shows that vicariance following a Gondwanan distribution is related to the present austral disjunct pattern in such woody forest taxa as *Araucaria* (Setoguchi et al., 1998), various groups of Cunoniaceae (Bradford & Barnes, 2001), and Winteraceae (Karol et al., 2000). The modern presence of species of *Araucaria* sect. *Araucaria* in South America and its sister group in Australia and New Zealand reflects their ancient Gondwanan history (Setoguchi et al., 1998). Obviously

the flora of southern South America was quite different at the beginning of the Tertiary; the early Cenozoic flora of this region consisted of proportionately more Gondwana elements than the present flora. The modern component of the flora that still reflects this relationship consists primarily of various conifers and other trees of the southern forests as pointed out by Arroyo et al. (1996). In contrast, most of the austral disjunctions we observe today occur in herbaceous or shrubby genera, and their biogeographic patterns are primarily the result of long-distance dispersal in the latter half of the Cenozoic.

In 1963, Raven published what is still the most thorough article on New World amphitropical disjunct taxa. He focused on what appeared to be closely related species pairs or individual species that had amphitropical distributions. In this work, he divided the disjunct entities into bipolar disjuncts and temperate disjuncts. Within the latter group, he further divided taxa into species or species pairs with distributions in western North America, coastal western North America, eastern North America, or widespread throughout North America. From Raven's (1963) list of bipolar taxa, I scored 23 of the 30 bipolar taxa as the same species and seven as species pairs (with the caveat that some species names have changed and that purported species pairs may not be as closely related as previously thought). Raven's largest category of disjunct taxa was the group distributed broadly in western North America, with 95 species that also occurred in, or had closely related species that occurred in, South America. Of these only about 24 species and 26 species pairs occurred in *southern* South America (primarily in southern Chile). Of the 15 taxa he grouped as western coastal North America, six occurred in southern South America, and of the taxa with widespread distributions across North America (14), eight occurred in southern South America, mostly in Patagonia. None of his eastern North America category (6) occurred to a significant extent in the Southern Cone.

As suggested in earlier studies (Raven, 1963; Simpson & Todzia, 1990), there is an appreciable taxonomic similarity between the temperate regions of North and South America. In many cases, this has resulted from long-distance dispersal, predominantly from North to South America. There seems to be no instance of a successful dispersal to temperate North America of a genus now represented in southern South America by a single species. It is therefore apparent that, as suggested by Raven (1963): (1) most of New World amphitropical disjunctions resulted from a dispersal from North to South America, (2) there was little radiation in South America after colonization by North American immigrants (many of the species listed are the sole member of their genus in South America), (3) most of the colonizations have been recent, and (4) successful establishments have been into habitats similar to those in North America. Bipolar disjunct immigrations have been particularly successful, whereas no taxa from the eastern U.S.A. have successfully colonized similar latitudes in South America—undoubtedly because the habitats of the northeastern U.S.A. are so different from those of the eastern portions of southern South America. While interesting, many of the South American taxa that are the result of amphitropical dispersals from North America play a relatively minor role in the diversity of the southern South American flora.

Wen and Ickert-Bond's (2009) more recent analysis of amphitropical distributions based on molecular phylogenetic studies reinforced these conclusions. Their study contained more genera than listed in Tables 2–4 because several of the groups they included are distributed primarily or only in areas north of the southern tropic in South America. Among the genera in their study were two species pairs within *Prosopis* based on work by Bessega et al. (2006). A later study (Catalano et al., 2008) using more taxa did not find these to be species pairs, and *Prosopis* was therefore not included here as showing an amphitropical distribution.

It is not surprising that most studies to date indicate that the direction of dispersal for these amphitropical groups was from North America to South America. Given the differences of land area and the correlation of species numbers with area, the probability of north to south dispersal is much greater than the reverse. George Gaylord Simpson (1952) famously stated that given a probability (even a miniscule one) and enough time, the improbable happens. Hence with a higher probability and the same amount of time, successful colonizations were primarily from the north. Nevertheless, there are a few classic examples of successful long-distance dispersals from South to North America, such as *Larrea* and *Hoffmannseggia* and, perhaps, some *Prosopis* species pairs.

The tropical element is probably the most underrepresented in the studies collected here, probably due in part to the difficulties in obtaining adequate plant material. Moreira-Muñoz and Muñoz-Schick (2007) concluded in their study of Chilean Asteraceae that the majority belong to, or are derived from, tropical groups. However, their listing of tropical groups included *Perezia*, which actually has a southern South America origin despite the fact that most of the species are found north of the Tropic of Capricorn. In fact, much of the central high Andean flora probably has a temperate origin, either from South America or to a lesser extent from North America.

If we look at the total number of species of autochthonous genera involved in molecular studies to date, it is relatively small and, more importantly, few of the genera studied (*Nothofagus* and *Nassauvia* Comm. ex Juss. being among the exceptions) are important floristic groups in southern South America in terms of abundance. However, many of the dominant genera in this region, both in terms of numbers of species and often the number of individuals per unit area, undoubtedly arose in southern South America and diversified from there. For example, Asteraceae, particularly the Mutisieae, is a dominant family. *Perezia*, *Nassauvia*, and *Chaetanthera* Ruiz & Pav. (all Asteraceae) have molecular phylogenies (although the problem of rooting makes interpretation of *Chaetanthera* problematic and so it was not included), and all indicate origins in temperate South America (Table 6). There is no doubt that other important genera in the Mutisieae, such as *Leucheria* Lag., are also indigenous to temperate South America. Apiaceae is another family of importance, particularly in Patagonia. Several recent phylogenies of umbelliferous genera with dominant species in southern South America (e.g., *Azorella* Lam., *Mulinum*; Table 6) have been published and again point to the rise of these groups in situ and their spread northward. Our data accumulated to date indicate that *Adesmia* (Fabaceae), another dominant group in Patagonia, originated in extratropical South America (Simpson et al., in prep.). Finally, *Malesherbia* and *Nolana*, both conspicuous and important groups in the temperate coastal deserts of South America, arose in the southern part of South America (Table 6).

It should also be pointed out that many genera listed in my tabulation as belonging to the austral distribution category arose in South America. As Table 7 shows, a third of the austral genera included appear to have arisen in South America but now have one or more species in Australasia. Perhaps these genera (such as *Ourisia*; see Table 1) should also be placed in the autochthonous group of South American genera (Table 6). All these findings indicate that the flora of southern South America has as major components, if not the major components, taxa that originated and/or diversified from autochthonous elements.

CONCLUSIONS

The flora of southern South America is unique and is a conglomerate of recent elements (mid-Tertiary to the present) that arrived via long-distance dispersal from the Northern Hemisphere and Australasia; old, Gondwanan elements; autochthonous elements that arose and diversified

in temperate South America; and Neotropical taxa that adapted to cold and/or dry conditions. Molecular phylogenies to date indicate that of these, north temperate elements are the most important contributors to the flora of southern South America. Nevertheless, the data compiled to date show that intercontinental relationships are complex, with relationships sometimes reflecting dispersal to southern South America and in other cases from South America. The data also suggest that the timings of exchange are variable and as yet do not show any pattern related to any particular times or events, although most dispersals of groups studied in detail are considered "recent."

One might argue that the flora of southern South America is ultimately all derived from tropical or warm temperate taxa since most of these genera eventually share an ancestor that occurred in tropical or subtropical habitats. These ancestral relationships, however, often predate the branching (origin) of what we now consider "genera" and the latitudinal temperature gradient and widespread dry conditions that now exist in southern South America. Moreover, the argument ignores the profound effects of the Tertiary and Pleistocene in selecting for new adaptive types, causing extinctions, promoting speciation with episodes of expansion and contraction, and providing habitats suitable for immigrants from similar northern or austral areas. It is these events, and not the suturing of an already developed temperate flora or an austral fragment with a tropical flora of a continental landmass, that led to the gradual development of a southern South American flora distinctive in physiognomy and floristic composition from that of the tropical regions to the north.

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PALEOBOTANY AND PALEOECOLOGY OF THE MUNCE'S HILL FOSSIL LOCALITY NEAR RED DEER, ALBERTA, CANADA

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ABSTRACT

The Munce's Hill locality in the Paskapoo Formation of south-central Alberta has yielded abundant well-preserved plant fossils of Late Paleocene (Tiffanian, Ti_4) age. This paper describes the flora and the stratigraphy of the site, revealing a wetland forest plant community that lived on a Late Paleocene floodplain. The fossils are found in two beds of silty mudstone that were deposited in a low-energy, relatively isolated environment. The plant assemblage is primarily autochthonous and is notable for seedlings in growth position. Fine details are preserved in many of the fossils, suggesting the original remains were buried rapidly before much degradation or transportation. The understory was dominated by *Equisetum* cf. *fluviatoides* McIver & Basinger, *Onoclea sensibilis L.*, and *Speirseopteris orbiculata* Stockey, Lantz & Rothwell. Successive fossil-bearing layers show a change in dominance of the forest canopy from *Metasequoia foxii* Stockey, Rothwell & Falder to the *Paleocarpinus joffrensis* Sun & Stockey, *Aphananthe* Planch. sp., *Wardiaphyllum daturaefolium* (Ward) Hickey, *Joffrea speirsiae* Crane & Stockey, and other angiosperms. More than 10 taxa are represented, some of which may be unique to the Paleocene of Alberta. The flora at Munce's Hill is most similar to that from the nearby, coeval Gao Mine site, but shows floral elements in common with Joffre Bridge and Burbank/Blindman in south-central Alberta, as well as several older Paleocene sites from Alberta, southern Saskatchewan, and North Dakota.

Key words: Flora, fossils, Paleocene.

The Munce's Hill fossil site in the Paskapoo Formation of south-central Alberta, Canada, is notable for well-preserved leaf litter and plant remains in growth position, including seedlings. Abundant plant macrofossils representing at least 10 identifiable taxa are now known from the Munce's Hill site. The wealth of material has permitted previous workers to complete whole-plant reconstructions for four taxa: foliage and reproductive structures of the ferns *Onoclea sensibilis* L. (Rothwell & Stockey, 1991) and *Speirseopteris orbiculata* Stockey, Lantz & Rothwell (2006), the

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betulaceous eudicot *Palaeocarpinus joffrensis* Sun & Stockey (1992), and the conifer *Metasequoia foxii* Stockey, Rothwell & Falder (2001).

The Late Paleocene (Tiffanian, Ti_4) age of the strata has been established by mammalian biostratigraphy (Krause, 1978; Fox, 1990), palynostratigraphy, and magnetostratigraphy (Lerbekmo et al., 1992), enabling correlation with other Paleocene fossil assemblages. In this paper we provide a detailed treatment of the complete Munce's Hill flora, with a description of the site's stratigraphy and an interpretation of the environment of deposition. The Munce's Hill flora is compared to other well-documented Paleocene plant fossil localities in the western Canadian interior, including the Joffre Bridge roadcut (Hoffman, 1995; Hoffman & Stockey, 1999), Gao Mine (Stockey et al., 2013), Smoky Tower (Christophel, 1976), and Genesee (Chandrasekharam, 1974) in Alberta, and Ravenscrag Butte in Saskatchewan (McIver & Basinger, 1993), and shows a few elements similar to the Golden Valley Formation of western North Dakota. The results show that Munce's Hill preserves a wetland forest plant community that lived on a Late Paleocene river floodplain.

MATERIALS AND METHODS

The Munce's Hill locality is a roadcut that lies approximately 9 km northeast of the city of Red Deer (Fig. 1), centered at about 52.3176°N, 113.6353°W. At the site, a section of bedrock up to 25 m thick is exposed for a distance of about 140 m along both sides of Alberta Township Road 390, where the road crosses the top of the hill. Plant fossils were primarily quarried from the base of the section on the north side of the roadcut. A mammal dentary previously came from the south side at this site (Fox, 1990). Strongly developed joint sets cut the rock at Munce's Hill into blocks that are typically smaller than about 15 cm on an edge; larger specimens could not be recovered intact and have been photographed in place (e.g., Rothwell & Stockey, 1991: plate 1; Stockey et al., 2001: fig. 2).

To facilitate description and measurement of the lithological units, five trenches were dug by hand, three on the north side of the roadcut and two on the south, to remove scree and weathered bedrock. Despite those efforts, it was not always possible to distinguish all detailed sedimentary features.

More than 18,000 compression/impression specimens (Table 1) from Munce's Hill are housed in the University of Alberta Palaeobotanical Collections (UAPC-ALTA) in Edmonton, Alberta, Canada. Specimens were photographed using a Microlumina digital scanning camera (Leaf Systems, Bedford, Massachusetts, U.S.A.) and formatted using Adobe Photoshop 7.0 (San Jose, California, U.S.A.).

GEOLOGICAL SETTING AND AGE

The Paleocene sediments of south-central Alberta are divided into the Upper Scollard Formation, which rests conformably on the Cretaceous/Paleogene boundary, and the Paskapoo Formation, which disconformably overlies it. Both were deposited by river systems that flowed eastward from the Cordillera (Gibson, 1977; Dawson et al., 1994; Eberth & O'Connell, 1995).

The fossil localities in the Red Deer area lie within the Paskapoo Formation, and their ages have been determined by mammalian biostratigraphy (Krause, 1978; Fox, 1990), supported by palynostratigraphic and magnetostratigraphic studies (Lerbekmo et al., 1992). Fox (1990) described mammal remains from a variety of localities in Alberta and Saskatchewan, including an incomplete mammalian dentary from Munce's Hill (which he referred to as "One Jaw Gap"). Fox determined North American land-mammal ages ranging from Middle to Late Tiffanian (Ti_3 to Ti_4) for the Red Deer area sites and assigned a probable age of Late Tiffanian (Ti_4) to Munce's Hill. Munce's Hill was

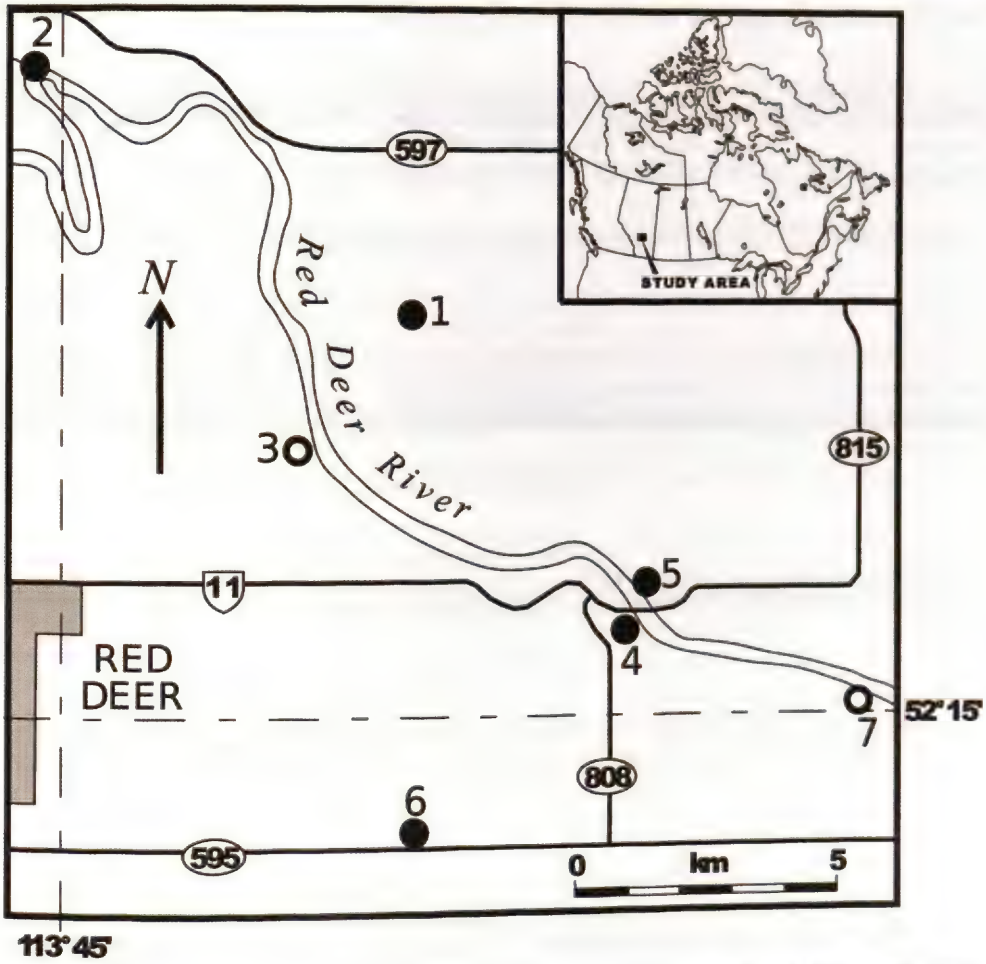

FIGURE 1. Red Deer area, showing location of Munce's Hill and other nearby fossil localities (modified from Hoffman, 1995). Open circles represent sites yielding plant fossils; filled circles represent sites yielding both plant and mammal fossils (mammal sites from Fox, 1990). —1. Munce's Hill (One Jaw Gap). —2. Burbank/Blindman. —3. Canyon Ski Quarry. —4. Joffre Bridge roadcut. —5. Erickson's Landing. —6. Gao Mine (Highway 595 roadcut). —7. Joffre Pipeline. Solid black lines represent numbered highways.

placed in the *Pistillipollenites mcgregorii* Rouse (P5) palynostratigraphic zone of Demchuk (1990) and within polarity chron 25r by Lerbekmo et al. (1992; under the locality name "One Jaw Gap"), which puts it in the later part of the Late Paleocene. Eleven distinct beds that persist across the entire length of the roadcut were identified during the trenching at Munce's Hill (Fig. 2).

Unit 1 is the lowermost unit exposed at Munce's Hill (Fig. 2). It consists primarily of mudstone and silty mudstone, with minor lenses of fine-grained sandstone. The sediments show little evidence of rooting or paleosol development.

Unit 1 is highly fossiliferous and has yielded numerous specimens of *Equisetum* L., the ferns *Onoclea* L. and *Speirseopteris* Stockey, Lantz &

TABLE 1. Systematics of plant taxa from the Munce's Hill fossil locality.

Family	Taxon	Approximate no. of specimens	Unit
Ricciaceae	*Ricciopsis* cf. *speirsiae* Hoffman & Stockey	2	3
Equisetaceae	*Equisetum* cf. *fluviatoides* McIver & Basinger	450	1, 3
Dryopteridaceae	*Onoclea sensibilis* L.	3200	1
Thelypteridaceae	*Speirseopteris orbiculata* Stockey, Lantz & Rothwell	1300	1
Incertae sedis	small fern crozier	4	1
Cupressaceae	*Metasequoia foxii* Stockey, Rothwell & Falder	5000	1, 3
Betulaceae	*Paleocarpinus joffrensis* Sun & Stockey	5000	3
Cannabaceae (Celtidaceae)	*Aphananthe* Planch. sp.	650	3
Cercidiphyllaceae	*Joffrea speirsiae* Crane & Stockey	7	3
Cercidiphyllaceae	*Joffrea* Crane & Stockey fruit	1	3
cf. Bignoniaceae	winged fruit/seed	700	3
Incertae sedis	*Wardiaphyllum daturaefolium* (Ward) Hickey	330	3
Incertae sedis	highly serrated leaf	2	3
Incertae sedis	elongate serrated leaf	1500	3
Incertae sedis	large circular leaf	1	3
Incertae sedis	ovate leaf	2	3
Incertae sedis	small circular leaf	5	3
Incertae sedis	grooved fruit/seed	8	3
Incertae sedis	bract or bud scale	1	3
Incertae sedis	roots	4	3

Rothwell, and the conifer *Metasequoia foxii* and its seedlings. Most of the material is in good condition and shows little evidence of transport. Some of the *Equisetum* and *Onoclea* specimens and most of the *Metasequoia* Hu & W. C. Cheng seedlings were preserved in growth position.

Unit 2 is a relatively thin but laterally continuous bed (0.05–0.20 m) of fine-grained sandstone that separates the fossiliferous mudstones of Units 1 and 3 (Fig. 2). The basal contact is sharp, and the top is gradational. Small amounts of plant material are present near the base.

Like Unit 1, Unit 3 is a highly fossiliferous mudstone, 0.65–1.60 m thick. The lower two thirds of Unit 3 are dominated by *Metasequoia* remains, including a layer of *Metasequoia* seedlings. Angiosperm leaves are abundant in the upper third. Leaves of *Palaeocarpinus* Crane dominate the assemblage, but those of *Aphananthe* Planch., *Wardiaphyllum* Hickey, and other angiosperms are also present. Most seedlings are in growth position and the leaves are in good condition. Unit 3 is capped by Unit 4, a fine-grained sandstone similar to Unit 2.

The upper units include beds of mudstone and silty mudstone (Units 5, 7, 9, and 11) that are separated by fine-grained sandstone layers (Fig. 2). There are also two very thin beds of shaly coal (Units 8 and 10). The mudstones are similar to those of Units 1 and 3, but they are not fossiliferous. There is evidence of rooting, and the plant material within them is limited to fine detritus and carbonaceous debris.

SYSTEMATIC PALEOBOTANY

FAMILY: RICCIACEAE

Genus: Ricciopsis Lundbl.

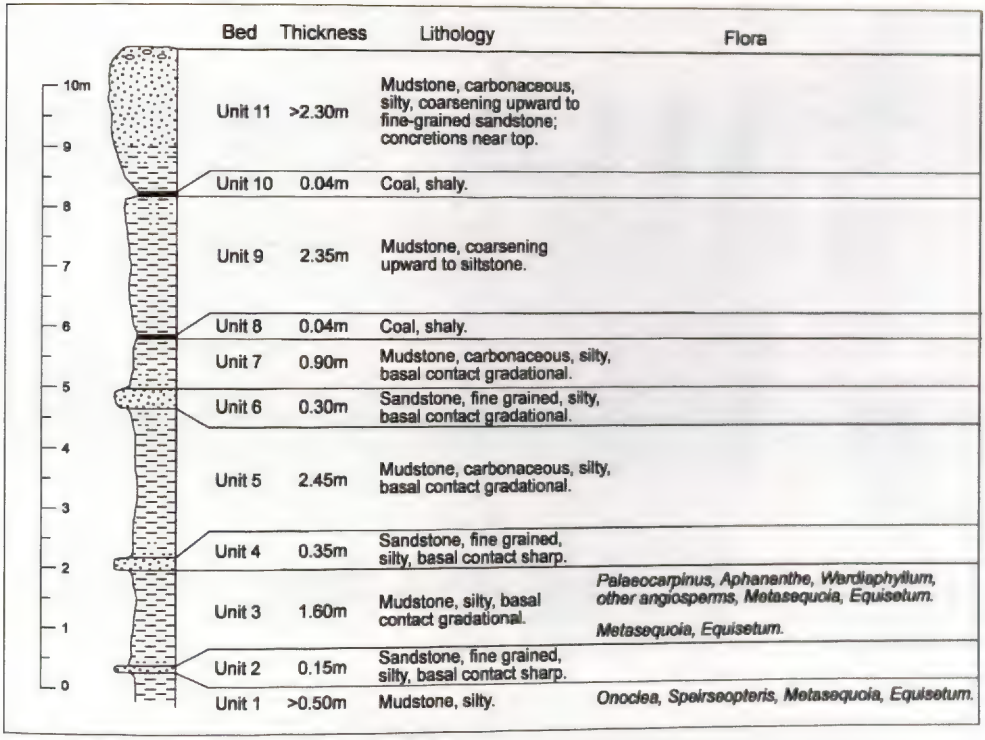

FIGURE 2. Stratigraphy at plant quarry site on north side of Munce's Hill roadcut.

Riccciopsis cf. speirsiae Hoffman & Stockey. Fossils consist of fragments of flat, ribbonlike, dichotomously branched thalli about 1.5–1.8 mm wide. The margins are smooth, and there are traces of a dorsal sulcus. The fragments are up to 5 mm long, and terminal segments are not preserved. These remains resemble *Ricciopsis speirsiae* from Joffre Bridge roadcut (Hoffman & Stockey, 1997), but are too poorly preserved to identify with certainty. There are only two specimens, both from Unit 3. They are not illustrated due to their poor condition.

FAMILY: EQUISETACEAE

Genus: *Equisetum* L.

Equisetum cf. fluviatoides McIver & Basinger (Fig. 3A–D). The material consists of stems with whorled leaves, rhizomes, and tubers recovered from Units 1 and 3. Stems are 2–15 mm wide, with internodal lengths of 10–45 mm, and a large central canal up to 6 mm in diameter (Fig. 3C). Leaves are typically in sheaths of 10, but some rare examples appear to have as many as 28, with the top quarter of the leaf free (Fig. 3A, B). Sheaths are often found isolated. Each individual leaf is 2–16 × 0.5–2 mm, with a prominent midvein. Rhizomes are 1–6 mm in diameter and 10–50 mm in internodal length, with branches and roots arising from the nodes. The most commonly found parts of these plants are the tubers, which are spherical and 4–12 mm in diameter. They typically occur in pairs, branching from rhizomes at the nodes (Fig. 3D). No strobili have been found.

Equisetum fluviatoides is very similar to modern *E. fluviatile* L., and so is presumed to have

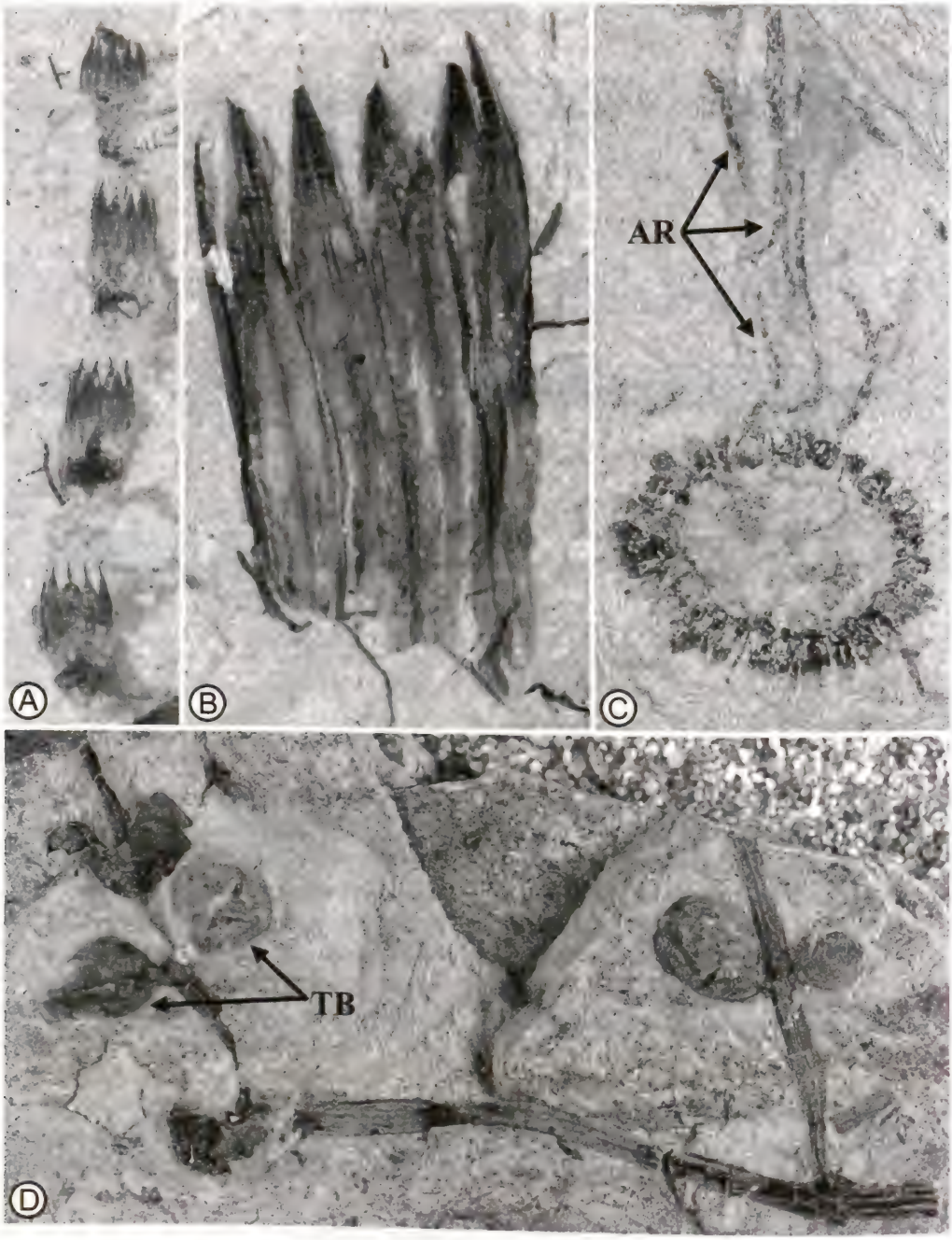

FIGURE 3. *Equisetum* cf. *fluviatoides* from Munce's Hill. —A. Degraded axis with four leaf sheaths. UAPC-ALTA S33,903A ×3. —B. Leaf sheath showing fusion of leaves and prominent midvein. UAPC-ALTA S36,584 ×6. —C. Cross section through rhizome with adventitious roots (AR). UAPC-ALTA S59,477 ×5. —D. Underground rhizome with branching at nodes and tubers (TB) arranged in pairs. UAPC-ALTA S58,739 ×1.8.

lived in similar growth conditions (McIver & Basinger, 1989). *Equisetum fluviatile* is known from the Northern Hemisphere from approximately 40°N–70°N latitude. It grows in wet areas with good sunlight, sometimes in standing water (Hauke, 1978); it is likely that similar growth conditions existed at Munce's Hill.

Despite the similarities, the fossil *Equisetum fluviatoides* differs from modern *E. fluviatile* in several ways. According to Hauke (1978), *E. fluviatile* does not produce tubers like those that are common at Munce's Hill. McIver and Basinger (1989) suggested that the lack of tubers may be a derived character of *E. fluviatile*. In addition, *E. fluviatile* often has branching stems, but there is no evidence of branching in any of our specimens that bear leaves. Several branching specimens were found, but due to lack of attached leaves or tubers, we were unable to determine whether these were vertical stems or horizontal rhizomes.

Equisetum fluviatoides shows a close resemblance to the fossil species *E. arcticum* Heer. However, the description of *E. arcticum* is incomplete and the material referred to the species is poorly preserved (McIver & Basinger, 1989). Further investigation and comparison of the two species may show that they are conspecific, at least in part, since a large number of poorly preserved specimens have been referred to *E. arcticum* (McIver & Basinger, 1989).

Equisetum remains are common in Units 1 and 3 at Munce's Hill, and it must have been a well-established member of the plant community. The common occurrence of underground tubers and cross sections of vertical stems indicates that many of the plants were preserved in situ or were not transported very far. Unfortunately, although Munce's Hill has yielded more than 450 specimens of *Equisetum*, strobili, which might allow a more definite identification, have not been found.

FAMILY: DRYOPTERIDACEAE

Genus: *Onoclea* L.

Onoclea sensibilis L. (Fig. 4A–C). The material consists of vegetative and fertile fronds from Unit 1. Because the fossil *Onoclea* from Munce's Hill is so completely known (including the spores), Rothwell and Stockey (1991) were able to show that it is identical in form to modern *O. sensibilis*, thus providing an excellent example of evolutionary stasis in ferns. Modern *O. sensibilis* inhabits marshes and swamps in eastern North America and eastern Asia (Lloyd, 1971; Tryon & Tryon, 1982). Macro- and microfossils of several species of *Onoclea* have been recovered from Paleogene sediments across North America (Ward, 1887; Hollick, 1936; Hickey, 1977; Rothwell & Stockey, 1991; Kvaček & Manum, 1993; McIver & Basinger, 1999).

FAMILY: THELYPTERIDACEAE

Genus: *Speirseopteris* Stockey, Lantz & Rothwell

Speirseopteris orbiculata Stockey, Lantz & Rothwell (Fig. 4D–F). Specimens consist of vegetative and fertile material from Unit 1. Munce's Hill is the type locality for this genus and species (Stockey et al., 2006), and about 1300 specimens of fertile (Fig. 4F) and sterile (Fig. 4D, E) pinnae have been found. However, all specimens are fragmentary, due to the fractured nature of the rock; until complete specimens are exposed in situ, the dimensions of the fronds cannot be established. The assignment of *S. orbiculata* to Thelypteridaceae is somewhat tentative, as the specimens also share many characters with Dryopteridaceae (Stockey et al., 2006). Nonetheless, *S. orbiculata* is one of the best-known species of compressed fossil ferns due to the large number of well-preserved specimens (Stockey et al., 2006).

Four specimens of a small, coiled fern crozier, 10–12 mm in diameter, have been recovered from Unit 1, but due to the lack of preserved diagnostic features, a definite identification is not possible. Based on the relatively small size, they are likely from *Speirseopteris orbiculata* (Fig. 4G).

FIGURE 4. Ferns from Munce's Hill. —A. *Onoclea sensibilis*, vegetative frond with pinnate-pinnatifid arrangement. UAPC-ALTA S35,721A ×0.8. —B. *Onoclea sensibilis* showing details of vegetative frond; note lonchopteroid venation. UAPC-ALTA S58,644 ×3.7. —C. *Onoclea sensibilis*, fertile frond with inrolled pinnules. UAPC-ALTA S58,667 ×1.4. —D. *Speirseopteris orbiculata*, sterile frond with twice-pinnate arrangement. UAPC-ALTA S26,917 ×1.1. —E. *Speirseopteris orbiculata*, sterile pinna. UAPC-ALTA S58,798B ×1.6. —F. *Speirseopteris orbiculata*, fertile pinna with sori at ends of veins. UAPC-ALTA S58,792 ×2.5. —G. Fern crozier UAPC-ALTA S59,476 ×4.

FAMILY: CUPRESSACEAE

Genus: *Metasequoia* Hu & W. C. Cheng

Metasequoia foxii Stockey, Rothwell & Falder (Fig. 5A–E). Specimens consist of branches, foliage, pollen and seed cones, dispersed and germinating seeds, and seedlings from Units 1 and 3. Most of the mature *Metasequoia* organs were found within Unit 1, while seedlings were found primarily in Unit 3.

Metasequoia foxii from Munce's Hill is a relatively newly named species (Stockey et al., 2001). At one time there were numerous specific names for fossil *Metasequoia*, but most of the extinct species have since been synonomized with *M. occidentalis* (Newberry) Chaney, leaving only the extinct *M. occidentalis, M. foxii, M. milleri* Rothwell & Basinger, and the extant *M. glyptostroboides* Hu & W. C. Cheng as formally recognized species (Liu et al., 1999; LePage et al., 2005).

The main distinguishing characters for *Metasequoia foxii* are the elongated leaves, the helical arrangement of cone scales, and a lack of shoot dimorphism. These characters are subtle, so the various species can easily be confused with one another unless a large number of specimens is available for study (Falder et al., 1999; Stockey et al., 2001). This was possible because Munce's Hill has yielded approximately 5000 specimens, and additional specimens have come from the nearby Gao Mine site (Fig. 1). *Metasequoia foxii* must have been very common at Munce's Hill in the Late Paleocene, and due to its deciduous habit and relatively rapid rate of burial, it left an unusually complete fossil record.

FAMILY: BETULACEAE

Genus: *Palaeocarpinus* Crane

Palaeocarpinus joffrensis Sun & Stockey (Fig. 6A–F). Remains of *Palaeocarpinus* have been found primarily in Unit 3. It is one of the most common fossils at Munce's Hill, and virtually the entire plant is represented, including inflorescences, infructescences, seeds, bracts, leaves, and branches.

Palaeocarpinus Crane (1981) was first described from the Paleocene of England and has also been identified in sediments across North America and northwestern China (Manchester & Chen, 1996; Manchester & Shuang-Xing, 1996). *Palaeocarpinus* is assignable to the Coryloideae, but combines characters of several of the living genera and probably is similar to what might be predicted as a hypothetical common ancestor for subfamily Coryloideae (Crane et al., 1990; Pigg et al., 2003; Manchester et al., 2004).

Munce's Hill is the type locality for *Palaeocarpinus joffrensis*, and more than 5000 specimens have been collected. It is now also known from Alberta, Montana, North Dakota, and Wyoming (Manchester & Chen, 1996).

FAMILY: CANNABACEAE (CELTIDACEAE)

Genus: *Aphananthe* Planch.

Aphananthe sp. (Fig. 7A–C). These leaves that come from Unit 3 are elliptical to ovate, 35–150 × 25–105 mm, with an attenuate to acuminate apex. Leaf bases are typically symmetrical and cordate to rounded, and the petiole is 10–12 × 1 mm. Leaf margins are unlobed and serrate, and primary venation is pinnate with craspedodromous secondaries. Secondary veins branch off the midvein at about 30° and are alternate. Most secondaries bifurcate near the margin, with either branch entering a primary tooth. Tertiary veins are opposite, percurrent, and at a uniform obtuse angle (> 90°) to the midvein. Quaternary veins are freely ending and branched, and areoles are quadrangular to polygonal. The leaf margin is serrate and possesses primary and secondary teeth. Tooth spacing is irregular. Individual teeth are simple. Sinus shape is angular.

Paleocene leaves from Asia and North America with characters that definitively assign them to

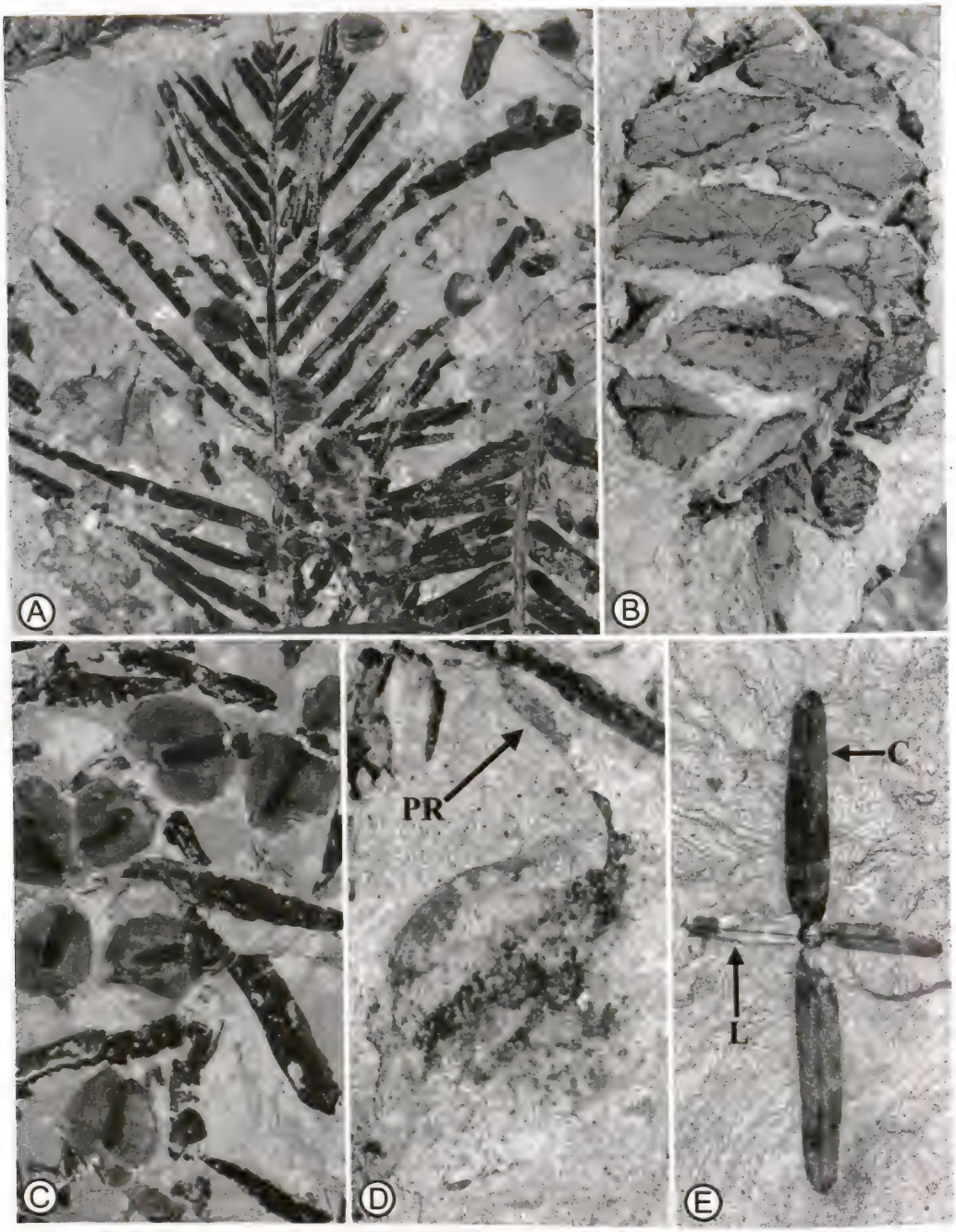

FIGURE 5. *Metasequoia foxii* from Munce's Hill. —A. Branch with elongate leaves. UAPC-ALTA S58,447 ×1.4. —B. Ovate ovulate cone. UAPC-ALTA S58,403 ×3.1. —C. Winged seeds. UAPC-ALTA S49,613 ×3.2. —D. Germinating seed; note primary root (PR). UAPC-ALTA S58,612 ×10. —E. Seedling with two cotyledons (C) and two juvenile leaves (L). UAPC-ALTA S51,537 ×2.4.

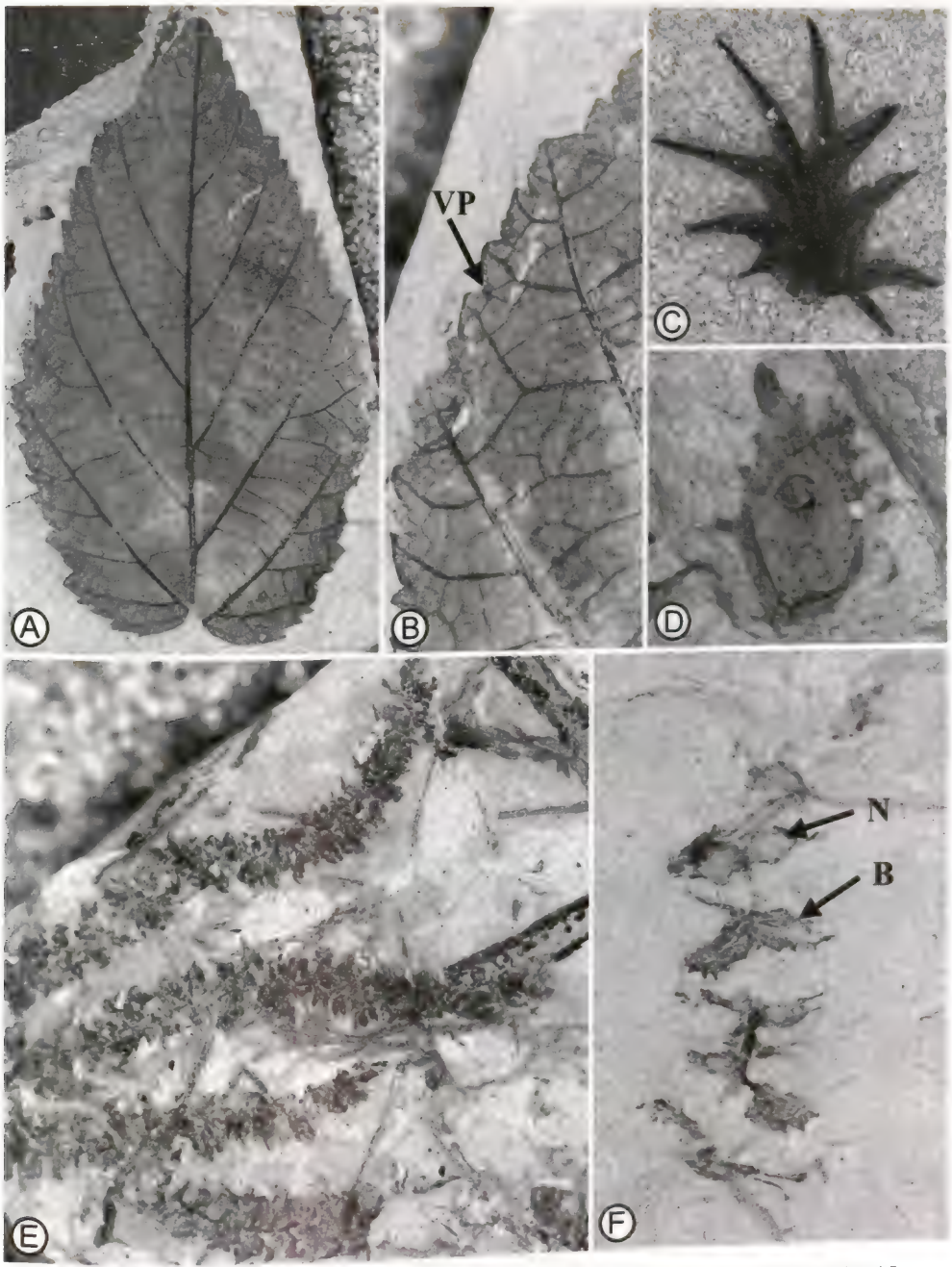

FIGURE 6. *Palaeocarpinus joffrensis* from Munce's Hill. —A. Leaf showing shape and venation. UAPC-ALTA S46,224 ×1.5 —B. Leaf margin showing marginal veins and teeth; note vein plexus in sinus (VP). UAPC-ALTA S48,514 ×3.5. —C. Bract showing shape and venation. UAPC-ALTA S45,641 ×14. —D. Dispersed nutlet with attached bract. UAPC-ALTA S50,019 ×15. —E. Staminate inflorescences. UAPC-ALTA S48,543A ×3. —F. Infructescence; note bract (B) and nutlet (N). UAPC-ALTA S58,569 ×7.

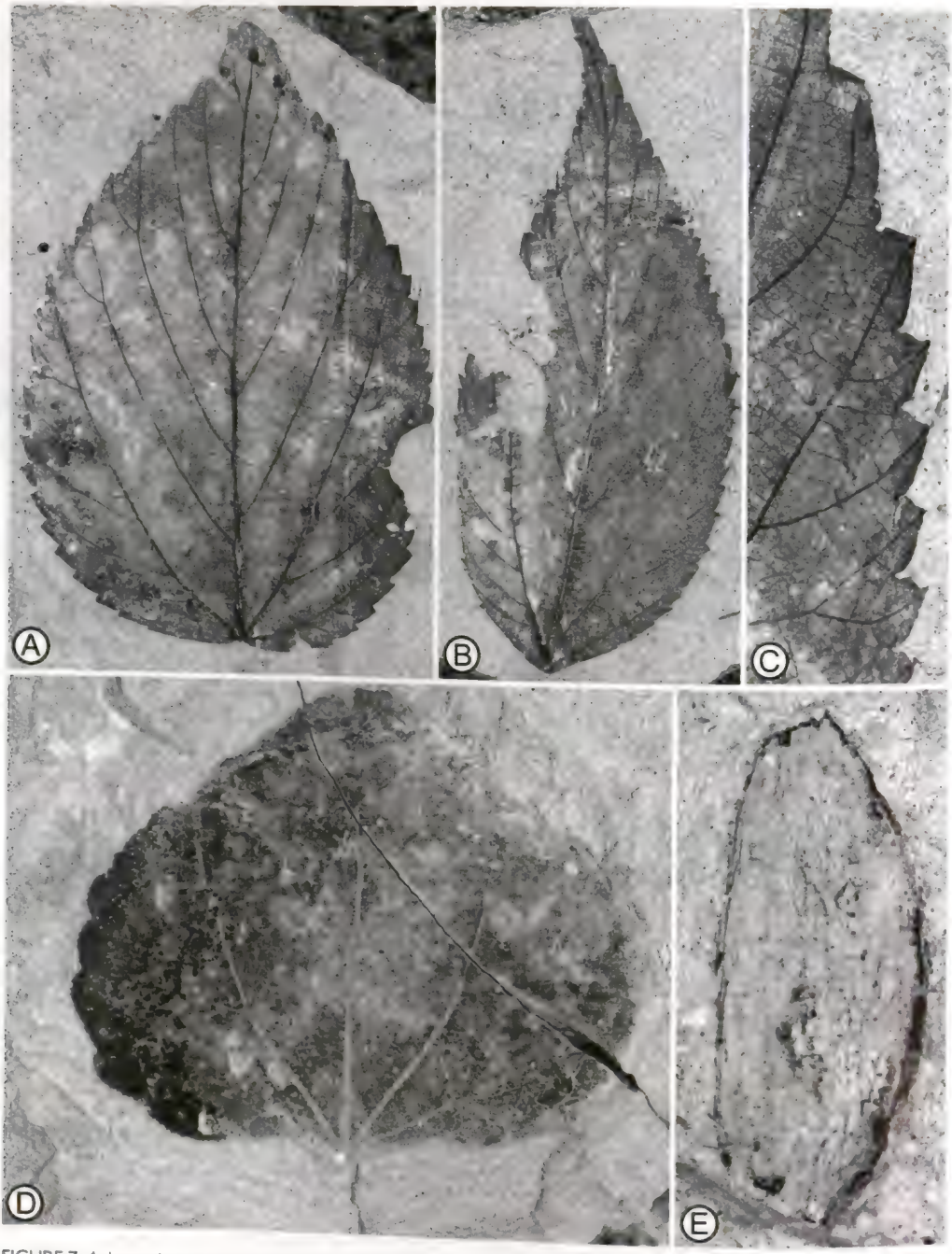

FIGURE 7. *Aphananthe* and *Joffrea* from Munce's Hill. —A. *Aphananthe* sp., ovate leaf showing venation. UAPC-ALTA S43,580 ×1.5. —B. *Aphananthe* sp., elliptical leaf showing venation. UAPC-ALTA S33,122 ×1.0. —C. *Aphananthe* sp., leaf margin showing marginal veins and teeth. UAPC-ALTA S43,580 ×3.5. —D. *Joffrea speirsiae*, leaf. UAPC-ALTA S59,334A ×2.6. —E. *Joffrea speirsiae*, follicle with longitudinal striations. UAPC-ALTA S45,168 ×8.

the Celtidaceaeae (currently classified in Cannabaceae; APG, 2009) were in the past often referred to the taxon *Viburnum asperum* Newberry (Manchester et al., 2002). It has been observed that *V. asperum* possesses a leaf morphology similar to that of modern *Aphananthe aspera* Planch., therefore Manchester et al. (2002) undertook a study to identify possible *Aphananthe* seeds and fruits from deposits where *V. asperum* had previously been recovered. They examined material from nine sites in North America and Asia and found endocarps diagnostic of *Celtis* L., but none of *Aphananthe* (Manchester et al., 2002). This led Manchester et al. (2002) to conclude that *V. asperum* was in fact a form of *Celtis*, and that the *Aphananthe*-like characters of the leaf morphology may be the ancestral condition for the group. *Viburnum asperum* was then reassigned to *C. aspera* Brongn. (Manchester et al., 2002).

The overall morphology of the leaves from Munce's Hill is similar to that of *Celtis aspera*, but the venation more closely resembles that of living *Aphananthe*; therefore, we treat these leaves as *Aphananthe*. In *Celtis*, the tertiary veins are looped and the tooth is supplied by a branch from this loop. In *Aphananthe*, as in the leaves from Munce's Hill, the secondary veins and tertiary veins enter the tooth directly without forming loops near the margin (see Manchester et al., 2002, figs. 6E–G). Manchester has identified one *Celtis*-like endocarp at Munce's Hill (S. R. Manchester, pers. comm., 2012), but none of *Aphananthe*. While this leaf type may be the ancestral type for the family, as Manchester et al. (2002) suggested, whole plants need to be reconstructed before the affinities of the leaf type present at the Alberta localities can be decided for certain. From what we know about fossils from closely related taxa in other angiosperm families (see Crane & Stockey, 1986), the attachment of inflorescences and fruits, and growth habit, often determine generic affinities of fossil organs in taxa with similar leaves.

FAMILY: CERCIDIPHYLLACEAE

Genus: *Joffrea* Crane & Stockey

Joffrea speirsiae Crane & Stockey (Fig. 7D, E). These leaves and fruits, found in Unit 3, represent the extinct eudicot *Joffrea speirsiae*. This taxon was originally described from the slightly older Late Paleocene (Tiffanian, Ti_3) Joffre Bridge roadcut locality (Fig. 1; Crane & Stockey, 1985), where its fossils are very common (Hoffman, 1995; Hoffman & Stockey, 1999). It is also present at the nearby Gao Mine (Stockey et al., 2013) and Burbank/Blindman localities (Table 2). *Joffrea* is relatively rare at Munce's Hill, however, where only about seven leaves have been recovered to date.

Elliptical fruits are 12–15 × 5–6 mm (Fig. 7E) with faint longitudinal striations. Fruits are very similar to the follicles of *Joffrea speirsiae*, but none have been found in attachment at Munce's Hill.

FAMILY: INCERTAE SEDIS

Genus: *Wardiaphyllum* Hickey

Wardiaphyllum daturaefolium (Ward) Hickey (Fig. 8A–D). These leaves from Unit 3 are simple and ovate to wide elliptic, about 45–80 × 35–80 mm. Apices are acute to acuminate, and bases are truncate, becoming decurrent near the long, stout petiole. Venation is pinnate and semicraspedodromous. The midvein is straight and of moderate thickness, and secondary veins branch off at angles of 40°–45°. Secondary veins are opposite decurrent to alternate decurrent. Tertiaries are thin, oppositely to alternately branched, and at a uniform obtuse angle (> 90°) to the midvein. Quaternary veins are very thin, reticulate, and form pentagonal areoles. Higher order veins branch once or twice with freely ending veinlets. A fimbrial vein is present. The leaf margin is unlobed and serrate, with very large, widely spaced teeth.

TABLE 2. Comparison of Paleocene floras from localities in Alberta (AB) and Saskatchewan (SK).

	South-Central AB				Northern AB	Central AB	Southern SK
	Munce's Hill	Gao Mine[1]	Joffre Bridge[2]	Burbank/ Blindman[1]	Smoky Tower[3]	Genesee[4]	Ravenscrag[5]
	Paskapoo Formation	Paskapoo Formation	Paskapoo Formation	Paskapoo Formation	Scollard Formation	Scollard Formation	Ravenscrag Formation
Taxa	**P5[6]**	**P5**	**P4**	**P4**	**P3**	**P1**	**P1**
Ricciopsis	×		×				
Onoclea	×	×			×		×
Speirseopteris	×	×					
Metasequoia	×	×	×	×	×	×	×
Paleocarpinus	×	×		×			
Aphananthe	×	×			×		
Joffrea/*Cercidiphyllum* Siebold & Zucc.	×	×	×	×	×	×	×
Wardiaphyllum	×	×	×				
cf. bignoniaceous fruit	×						
Elongate serrated leaf	×						

[1] UAPC-ALTA catalog.
[2] Hoffman (1995).
[3] Christophel (1976).
[4] Chandrasekharam (1974).
[5] McIver and Basinger (1993).
[6] Palynostratigraphic zones are indicated by P5, etc., and follow Demchuk (1990).

Teeth are narrow, have acute tips (< 90°) and appear glandular with rounded sinuses (Fig. 8B).

Leaves with this morphology were originally described by Ward (1887) as "?*Credneria daturaefolia*" Ward. Cockerell (1908) noted a resemblance to *Populus* L., and Bell (1949), who collected similar leaves about 150 km west of Munce's Hill, assigned them to *P. daturaefolia* (Ward) Cockerell. Hickey (1977) erected the genus *Wardiaphyllum* for them, mentioning that the leaves bear some similarities to those of Platanaceae in tooth morphology and in tertiary and quaternary venation patterns. *Wardiaphyllum daturaefolium* remains the only species in this genus, and its affinities will likely remain undetermined until reproductive organs of this plant are recognized.

Unit 3 at Munce's Hill has yielded approximately 330 specimens of *Wardiaphyllum* leaves; the large number of specimens provides insight into the range in morphology that is typical of these leaves. Some are complete, with well-preserved glandular teeth not seen in specimens from other sites. Damage probably caused by insect galling (e.g., Labandeira et al., 2007) is present on many of the specimens from Munce's Hill (Fig. 8B) and appears to be typical for this taxon, since it is also seen on specimens from the Late Paleocene beds of the Golden Valley Formation (Hickey, 1977: plate 52, 2; plate 53, 1), and on specimens from Joffre Bridge roadcut (Hoffman, 1995: plate 11, 83) and the Gao Mine (Stockey et al., 2013). Munce's Hill appears to be unique in the large numbers of *Wardiaphyllum* specimens and range of sizes preserved.

FAMILY: INCERTAE SEDIS

Highly serrated leaf (Fig. 9A, B). The leaves are elliptic to ovate, 55–70 × 45–50 mm, with an acute to attenuate apex and an obtuse to rounded

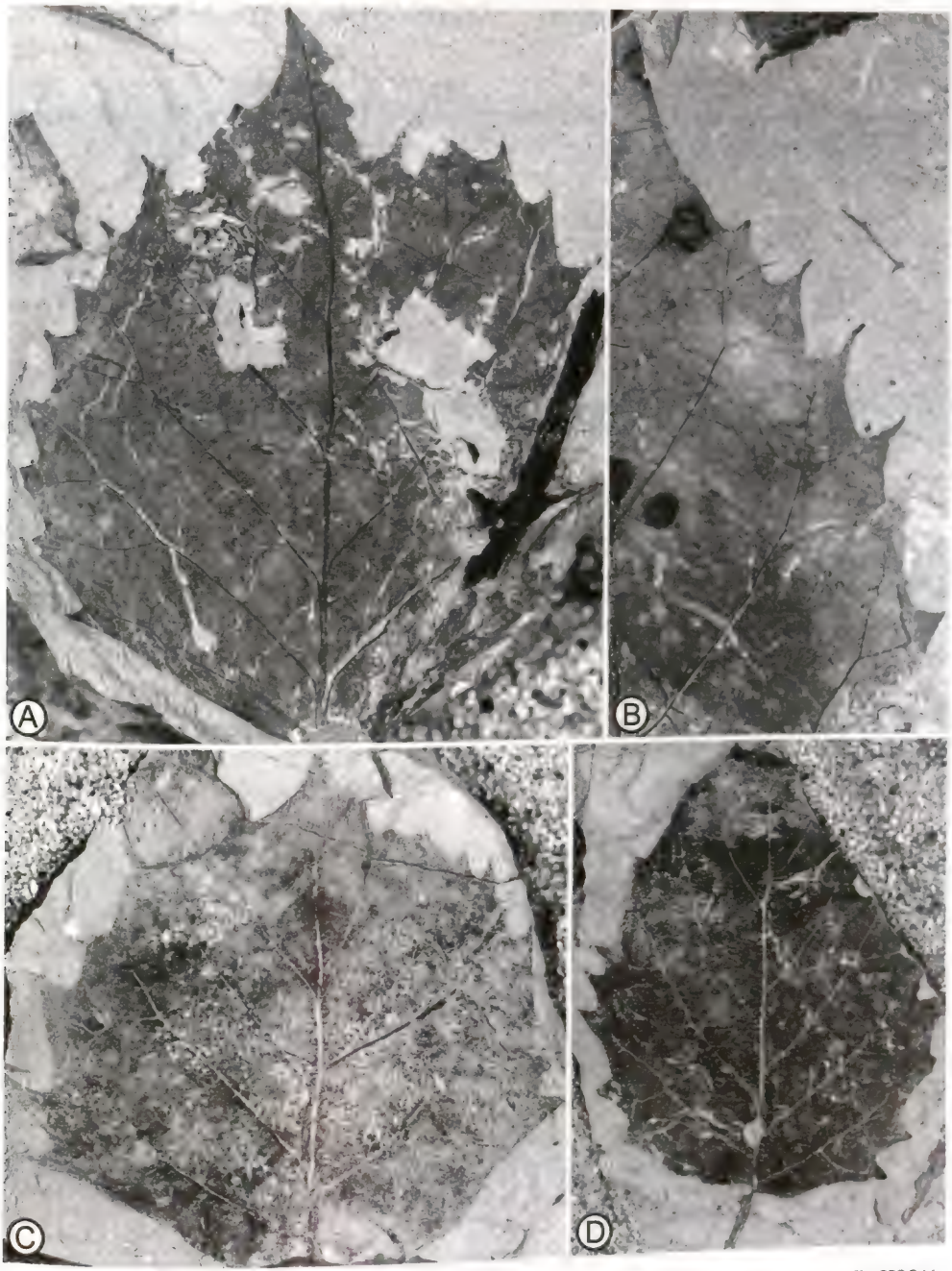

FIGURE 8. *Wardiaphyllum daturaefolium* from Munce's Hill. —A. Leaf with subopposite secondary veins. UAPC-ALTA S33,266 ×2. —B. Leaf margin with glandular teeth and possible insect galls. UAPC-ALTA S44,958 ×2. —C. Leaf. UAPC-ALTA S48,637B ×0.9. —D. Leaf with alternately arranged secondary veins. UAPC-ALTA S50,755 ×0.9.

base. Venation is pinnate and craspedodromous, with two pairs of crowded basal secondaries. Tertiaries are sinuous, alternate percurrent, and at an inconsistent obtuse angle (> 90°) to the midvein. Quaternaries are random reticulate and have freely ending veinlets. Areoles are polygonal, and the leaf margin is lobed serrate. There are primary, secondary, and tertiary teeth, with simple primary teeth. Sinuses are rounded or angular.

This leaf has a much more serrate margin than *Palaeocarpinus*, with two pairs of crowded basal secondaries. Also, no vein plexus could be seen in the sinuses. Primary teeth appear platanoid in some well-preserved specimens (Fig. 9B).

FAMILY: INCERTAE SEDIS

Elongate serrated leaf (Fig. 9C, D). The leaves are elliptical to ovate, with an acute to attenuate apex and cuneate leaf base. Leaves are from 28 to > 100 × 10–45 mm (length:width = 3:1). Margins are unlobed and serrate, and venation is pinnate and craspedodromous. Secondaries arise at an angle of 30°–40°, are uniform in spacing, and are arranged oppositely, suboppositely, or alternately. Secondary veins dichotomize near the margin. Tertiary veins are random reticulate and sinuous, and quaternary veins branch one to three times with free ends. Areoles are polygonal, and a fimbrial vein is present. Only simple primary teeth are present; they are regularly spaced with an angular sinus.

This appears to have been a rather thin leaf, and fine details of the venation are rarely preserved. Approximately 1500 specimens have been collected, primarily from Unit 3, but none have been found attached.

FAMILY: INCERTAE SEDIS

Large circular leaf (Fig. 9E). One circular leaf, 22 mm in diameter, with a cordate base, has been recovered. Venation is pinnate, craspedodromous, with crowded basal secondaries. Tertiary veins are opposite to alternate percurrent, with polygonal areoles. The margin is unlobed and serrate with simple primary teeth. Only one specimen of this leaf is known, and due to the lack of apex and well-preserved petiole region, we cannot assign it to any taxon at this time.

FAMILY: INCERTAE SEDIS

Ovate leaf (Fig. 10A). An ovate leaf, 33 × 20 mm, with an acute apex and a cordate base, has been recovered. Venation is pinnate, craspedodromous, with alternate secondaries. Tertiaries are sinuous and alternate percurrent, and areoles are polygonal. The margin is unlobed and serrate, and only simple, primary teeth are present. Sinuses are angular and tertiaries and quaternaries form a plexus in the sinus.

These leaves may be young betulaceous leaves since they show several sinuses that have a plexus of tertiary and quaternary veins, like those seen in *Palaeocarpinus*. There are only two specimens and preservation of the finer venation is not good, so it is difficult to tell if they are betulaceous.

FAMILY: INCERTAE SEDIS

Small circular leaf (Fig. 10B). Five specimens of a small, circular leaf with entire margins, 10–11 mm in diameter, with basal, reticulate, actinodromous primary venation have been found. Secondary veins are anastomosing, and tertiary veins are random reticulate. There appears to be a thin fimbrial vein. Areoles are polygonal, and highest order veins are freely ending. We cannot assign these leaves to any known taxon at this time. However, based on the size, shape, and presence of a fimbrial vein, they may have belonged to an aquatic plant.

FAMILY: INCERTAE SEDIS

Grooved fruit or seed (Fig. 10C). Elliptical fruits/seeds, 15 × 7 mm, with two or three prominent longitudinal grooves, have been recovered. Only about 8 specimens are known.

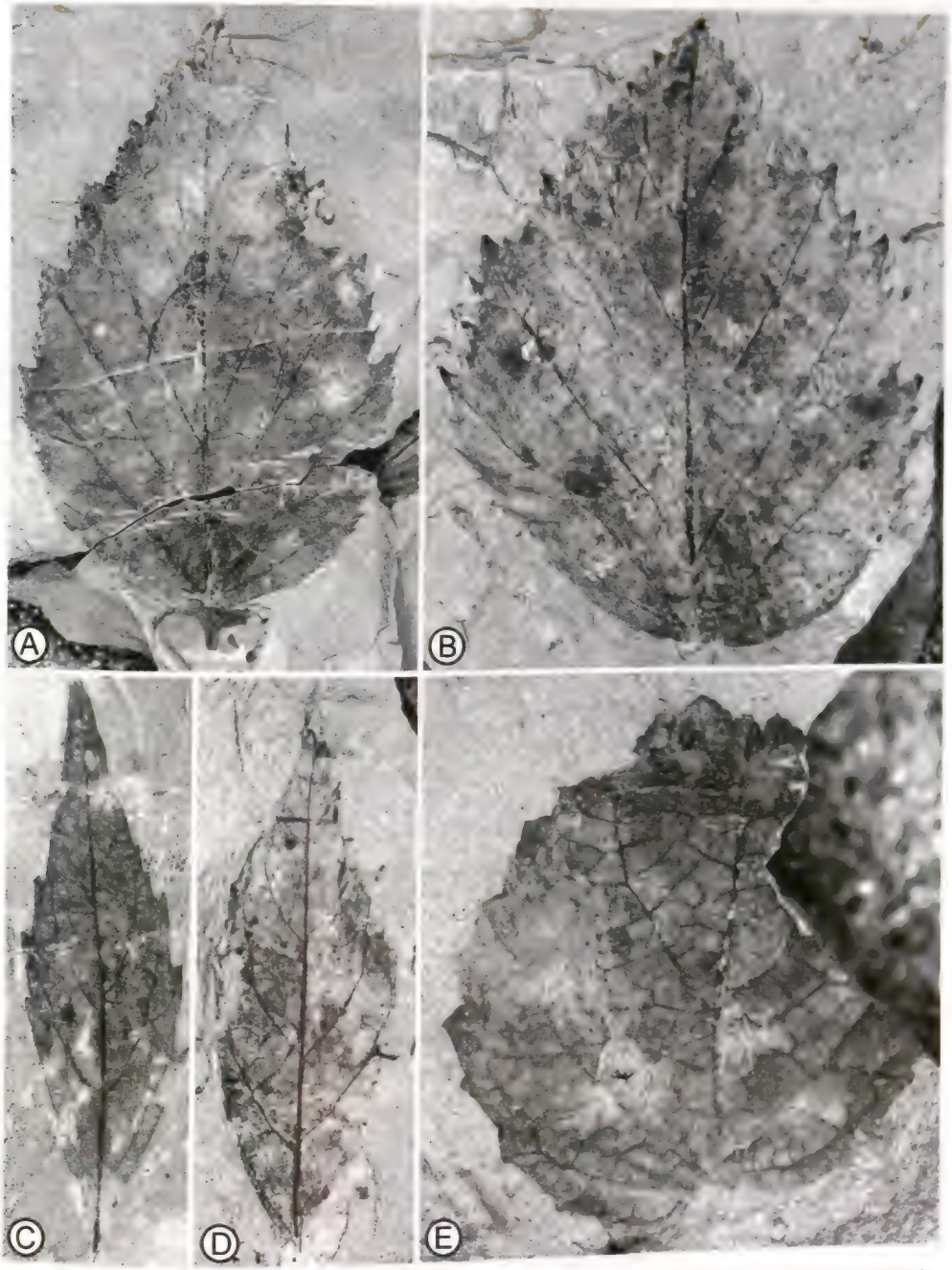

FIGURE 9. Angiosperm leaves from Munce's Hill. —A. Highly serrated leaf. UAPC-ALTA S48,762B ×1.4. —B. Highly serrated leaf; note lobes with different sized teeth. UAPC-ALTA S59,387 ×2.2. —C. Elongate, serrate leaf with subopposite secondary veins. UAPC-ALTA S59,478 ×4.0. —D. Elongate, serrate leaf. UAPC-ALTA S32,112 ×3.5. —E. Large circular leaf. UAPC-ALTA S59,402 ×4.5.

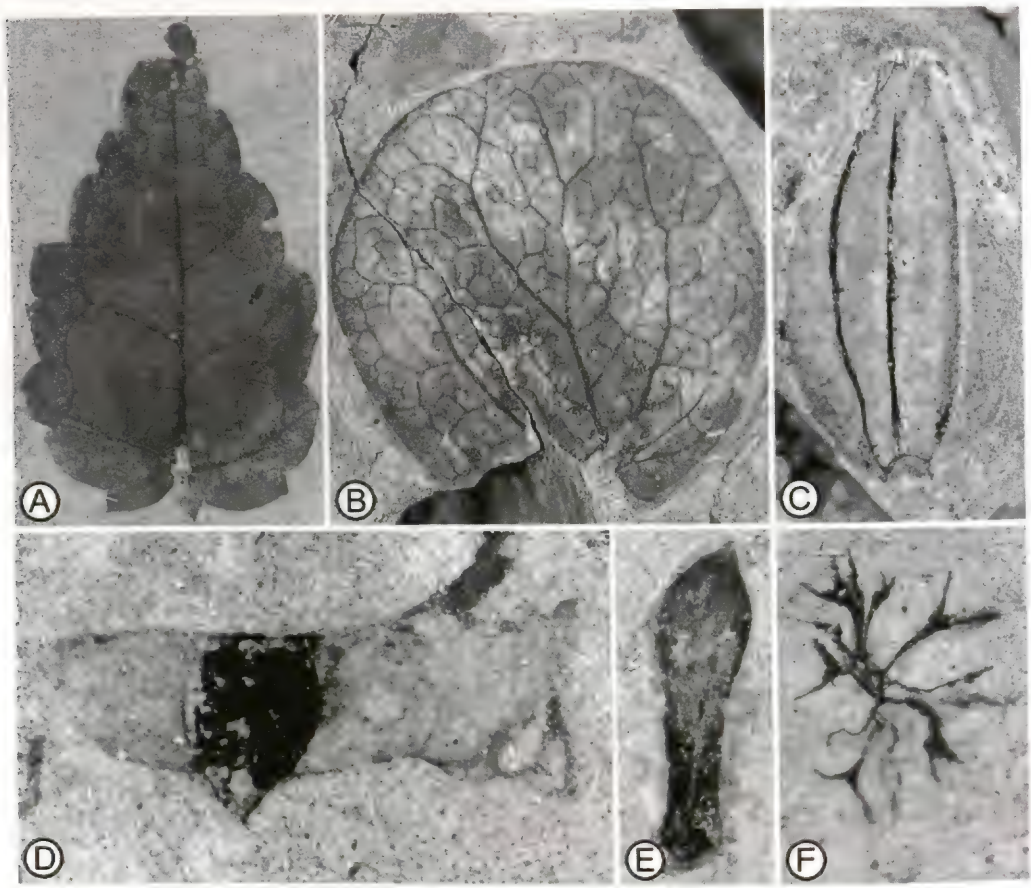

FIGURE 10. Leaves, fruits, seeds, bracts, and roots from Munce's Hill. —A. Ovate leaf. UAPC-ALTA S59,333A ×2.3. —B. Small circular leaf. UAPC-ALTA S59,443B ×9.0. —C. Grooved fruit or seed. UAPC-ALTA S59,440 ×5.5. —D. Unidentified fruit with teardrop-shaped body and two lateral wings. UAPC-ALTA S45,919 ×14. —E. Unidentified bract or bud scale. UAPC-ALTA S59,479A ×4.5. —F. Root cluster. UAPC-ALTA S59,393 ×6.

FAMILY: CF. BIGNONIACEAE

Winged seed or fruit (Fig. 10D). These fruits or seeds have a teardrop-shaped seed body or nutlet, with two oppositely arranged wings. The body is 3 × 2 mm, and the wings are each 2–3 × 2–4 mm. Approximately 700 fruits/seeds of this type have been cataloged. It is possible that these are single-seeded fruits with wings. Two-winged fruits have been reported in Betulaceae in both *Betula* L. and *Alnus* Mill. (Chen et al., 1999), but we have not found a pair of styles attached to any of the specimens, as are seen in fruits of Betulaceae (Crane & Stockey, 1987). The specimens bear a resemblance to dispersed seeds of Bignoniaceae reported from the Paleocene of Montana (Brown, 1962) and the Eocene of Washington (Pigg & Wehr, 2002).

FAMILY: INCERTAE SEDIS

Unidentified bract or bud scale (Fig. 10E). A possible bract, 14 × 4 mm, obovate, is represented by a single specimen (part and counterpart).

FAMILY: INCERTAE SEDIS

Roots (Fig. 10F). Very fine, branching clusters of roots, approximately 3–4 mm across, occur in the Munce's sediments. These roots have not been found attached to any other material, and only about four specimens have been found.

DISCUSSION

FLORAL DIVERSITY

Based on sedimentology at Munce's Hill, the plant-bearing beds at the base of the outcrop, Units 1 and 3, were deposited on a rapidly aggrading floodplain. Sediments consist primarily of silty muds that would have accumulated in a low-energy depositional setting, such as a relatively isolated floodplain wetland. The beds of fine-grained sandstone, such as Unit 2, would have been introduced by floods, but the lack of coarser sandstones suggests that the site was not close to an active fluvial channel. Sedimentation rates must have been fairly high, because there is little evidence of soil formation or rooting in Units 1 to 3, and most of the plant remains were buried before significant degradation or transportation occurred.

The plant species and their taphonomy support this interpretation. The flora of Unit 1 consists primarily of *Onoclea*, *Speirseopteris*, and *Equisetum*, which represent the understory of a wetland forest, and dispersed organs and seedlings of *Metasequoia*, which represent the canopy.

The Unit 1 flora is primarily autochthonous, with some of the *Equisetum* and *Onoclea* specimens and most of the *Metasequoia* seedlings preserved in growth position. The unit represents an environment with moist soils and periodic flooding. Extant *M. glyptostroboides* thrives in moist forests (Chu & Cooper, 1950). *Metasequoia foxii* seedlings sprouted on moist sediments and were rapidly buried in growth position during flooding. Extant *Onoclea* and *Equisetum* are also found in moist forests and poorly drained soils, and along the shores of ponds and streams (Tryon & Tryon, 1982). *Onoclea* fronds at Munce's Hill have been found flattened on bedding planes a few centimeters above their rhizomes, and appear to have been swept over and buried intact (Rothwell & Stockey, 1991).

The Unit 2 sandstone that separates the fossiliferous mudstones of Units 1 and 3 was probably deposited by a flood, and may represent the distal portion of a crevasse splay. The increased grain size relative to Units 1 and 3 reflects a higher energy level in the environment of deposition at that time. The sharp basal contact and gradational top contact indicate that deposition began abruptly and ended more gradually. The Unit 4 sandstone that caps Unit 3 is quite similar and probably represents a similar event.

The sediments of Unit 3 are similar to those of Unit 1, but there is a change in the flora. *Metasequoia* remains, including seedlings in growth position, are common in the lower two thirds of the unit, but angiosperm leaves become dominant in the upper third. They include abundant leaves and reproductive structures of *Palaeocarpinus*, as well as leaves of *Aphananthe*, *Wardiaphyllum*, and other angiosperms. Above Unit 3 the sediments are mud-dominated like those of Units 1 and 3, but plant remains are limited to root traces, fine detritus, and carbonaceous matter.

The diversity of the flora is relatively low in comparison to those of other sites in the Red Deer area (Table 2), and other Paleocene and Eocene sites in the interior of North America (Pigg & DeVore, 2010). The local forest at Munce's Hill was dominated by one conifer and, later, by a few species of angiosperm trees, while the understory was dominated by *Equisteum* and two ferns. This low diversity probably reflects that only a single floodplain environment is represented at Munce's Hill, and the flora is primarily autochthonous with very little allochthonous material introduced from other environments, despite occasional floods. Higher diversity Late Paleocene assemblages are known from the nearby Joffre Bridge roadcut and

Burbank/Blindman localities (Fig. 1), but they encompass a wider variety of depositional environments, such as fluvial channels, shallow ponds, and swamps, in addition to floodplain settings (Hoffman & Stockey, 1999; G. L. Hoffman, pers. obs.).

Based on comparisons between the Munce's Hill flora and other floras from the Paleocene of Alberta and southern Saskatchewan, there appears to be a detectable turnover in floral composition through time (Table 2). Each flora is most similar to other floras closest in age, despite the large differences in total numbers of taxa from each site (Table 2). Although the exact pattern of the turnover is not readily obvious, it may be driven in part by changing ecological or environmental factors through the Paleocene.

Pigg and DeVore (2010: table 1) compared Late Paleocene (and Early Eocene) localities from North America with respect to floral composition and identified several taxa also seen at Munce's Hill as "key taxa." They included *Ricciopsis*, *Onoclea*, *Speirseopteris*, *Metasequoia foxii*, *Palaeocarpinus*, and *Joffrea* in their list. In central Alberta, *Wardiaphyllum* and *Equisetum* can also be added to this list. Pigg and DeVore (2010) point out that Tertiary paleobotanists have tended to focus on either paleoecology or systematics. The current paper is an attempt to provide data on both the systematics and depositional setting at the Munce's Hill site.

CONCLUSIONS

Despite the low diversity, Munce's Hill has made a significant contribution to our knowledge of the Paleocene flora of the western Canadian interior. Munce's Hill has provided the type material for three well-documented taxa: *Speirseopteris orbiculata*, *Metasequoia foxii*, and *Palaeocarpinus joffrensis*. Of these, *Speirseopteris* and *M. foxii* are known only from Munce's Hill and the nearby Gao Mine site (Table 2; Stockey et al., 2013). In contrast, *Palaeocarpinus* is now recognized from a variety of localities in western North America (Manchester & Chen, 1996; Pigg & DeVore, 2010). *Wardiaphyllum*, which is also present at Joffre Bridge roadcut (Table 2) and the Golden Valley Formation of South Dakota (Hickey, 1977), is now better documented due to the large number of specimens from Munce's Hill, as is the winged, possibly bignoniaceaeous seed, which is similar to dispersed seeds from the Paleocene of Montana (Brown, 1962) and the Eocene of Washington (Pigg & Wehr, 2002).

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HISTORICAL BIOGEOGRAPHY OF THE NEOTROPICAL LEGUME GENUS *DUSSIA*: THE ANDES, THE PANAMA ISTHMUS, AND THE CHOCÓ

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ABSTRACT

Phylogenetic relationships of species in the papilionoid legume genus *Dussia* Krug & Urb. ex Taub. were investigated using nuclear ribosomal internal transcribed spacers and chloroplast *trnL* and *trnD-T* DNA sequences. Bayesian phylogenetic dating techniques suggest that: (1) the uplift of the Andean Mountains created a biogeographical barrier to migration but also contributed to speciation; (2) migration between South America and Central America occurred before the closure of the Panamanian isthmus, indicating that for *Dussia* the Pacific Ocean was less of a barrier than the Andes; and (3) the biogeographic affinities of species from the Chocó biogeographical region are with Central America.

Key words: Leguminosae (Fabaceae), Neotropics, Papilionoideae, phylogeny, speciation.

The high diversity of plant species in Neotropical rainforests is well recognized, but the historical reasons underlying this species richness and its geographical distribution are not well understood (Hughes et al., 2013). The possible geological and climatic factors that may have influenced Neotropical diversification have been the subject of numerous reviews and include the uplift of the Andes, migration from Central America via the Isthmus of Panama, and Pleistocene climatic changes (e.g., Gentry, 1982a; Burnham & Graham, 1999; Hughes et al., 2013). In this paper we use the genus *Dussia* Krug & Urb. ex Taub. (Leguminosae [Fabaceae], Papilionoideae) as a case study to examine the influence of these factors, especially the Andean orogeny, on rainforest trees. In addition, and in particular, we examine the relationships of *Dussia* species found in the Chocó biogeographical region. The Chocó is home to the only rainforests found on the Pacific coast of South America and has been the subject of few molecular biogeographical studies.

THE CHOCÓ

The Chocó biogeographical region is characterized by lowland rainforest that stretches along the Pacific coast of western Colombia to northwestern Ecuador. It is one of the wettest places on earth, with a yearly average of > 11 m of rain

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(Gentry, 1982b), and is a species-rich center of plant endemism.

Understanding of the Chocó's biogeographic history is in its infancy because few phylogenies have included species from this region, and these have not examined the relationships of species found in the Chocó with relatives elsewhere in the Neotropics (e.g., Jaramillo, 2006). The key geological events to be considered in the biogeographic history of the Chocó are the orogeny of the Andes and the closure of the Panamanian isthmus. The lowland rainforests of the Chocó are physically isolated by the Andes to the east, the Pacific Ocean to the west, and by seasonally dry tropical forest (grading into the Atacama Desert) to the south (Gentry, 1982b; Prance, 1982). In the north, barriers to migration of lowland rainforest biota are less obvious. The low Serranía hills along the Panamanian border are covered in rainforest, but a terrestrial migration route for rainforest biota to and from Central America was not available until the closure of the Isthmus of Panama (see below). To the northeast are the drier forests of Caribbean coastal Colombia, which may serve as a barrier for some rainforest species (Honorio et al., 2014).

THE ANDEAN OROGENY

There is considerable debate about the exact timing of the Andean uplift (Sempere et al., 2008; Ehlers & Poulsen, 2009), but it is clear that the northern Andes were still relatively low (400–2500 m) about 10 million years ago (Ma; Quade et al., 2007; Thouret et al., 2007). This implies a recent, rapid uplift in the past 10 million years. Garzione et al. (2008) suggested progressive uplift of the Central Andes between ca. 40 and 10 Ma due to crustal and mantle thickening, followed by a single burst of uplift that increased elevation by 2.5 ± 1 km during the Late Miocene (ca. 10–6 Ma) across the entire width of the mountain belt below 5°S latitude. Other studies corroborate that the Western Cordillera of the Central Andes had reached no more than half of its present height by 25–18 Ma, while the Eastern Cordillera of the Central Andes had reached a maximum of half its present height by 10 Ma (Gregory-Wodzicki, 2000). Further north the uplift may have been even more recent (Gregory-Wodzicki, 2000). In Colombia, the Andes divide into the Eastern, Central, and Western Cordilleras. From the Middle Miocene through to the Early Pliocene, elevations in the northern Eastern Cordillera of the Andes were no more than 40% of their modern values, but between 2 and 5 Ma uplift occurred at a more rapid rate, reaching modern elevations by around 2.7 Ma (Gregory-Wodzicki, 2000).

Mountain formation creates new habitats, has an impact on climate, and can also create barriers to migration. The environmental changes associated with the recent orogenic events in the Andes Mountains have long been associated with hypotheses of rapid Neotropical evolution and speciation (Gentry, 1982a; Burnham & Graham, 1999; Richardson et al., 2001; Hughes & Eastwood, 2006; Antonelli et al., 2009; Hoorn et al., 2010). In addition, Andean uplift has been suggested as the cause of allopatric speciation, when populations of lowland species became isolated on either side of the cordillera. A classic and much cited example (e.g., Whitmore, 1998) is three genera and seven species of ivory vegetable palm that in northern South America are divided between three areas separated by the Cordilleras: western Amazonia, the Cauca and Magdalena valleys, and the Chocó. Pirie et al. (2006) showed that no species of *Cremastoperma* R. E. Fr., *Klarobelia* Chatrou, *Malmea* R. E. Fr., or *Mosannona* Chatrou (Annonaceae) are present on both sides of the Andes, and that divergence dates of clades separated by the mountains were consistent with the age of the Andean orogeny and therefore likely to have been the result of an allopatric speciation process.

The orogeny of the Andes also played a key role in changing climate because these mountains form the only barrier to atmospheric circulation

in the Southern Hemisphere (Gregory-Wodzicki, 2000; Hoorn et al., 2010). The growing Andean mountain chain enhanced aridification on the coasts of Peru and Chile ca. 9–15 Ma (Alpers & Brimhall, 1988; Houston & Hartley, 2003; Rech et al., 2006), which ultimately led to the appearance of the world's driest desert, the Atacama, which, along with ecotonal seasonally dry tropical forests, isolates the Chocó to its south. Seasonally dry climates found in the Caribbean coastal regions of northern South America also isolate the Chocó biotically. Seasonally dry forests and even semideserts are found along the Caribbean coast of Colombia, in addition to the Llanos grasslands that are found from the foothills of the Andes to the coast of eastern Venezuela. These seasonally dry vegetations may have served as barriers for the migration of wet-adapted taxa, a hypothesis that has received some support by strong genetic differentiation between Central American and Amazonian populations of Neotropical tree species confined to rainforests, such as *Ficus insipida* Willd. (Honorio et al., 2014).

THE ISTHMUS OF PANAMA

The formation of the Panamanian land bridge 3.4–3.1 Ma (Coates & Obando, 1996) connected North and South America and terminated the long period of isolation of South America through the Cenozoic (Simpson, 1980; Burnham & Graham, 1999). However, recent studies indicate that the land bridge may actually have begun to form from the Early Miocene (Farris et al., 2011; Montes et al., 2012). The land bridge was thought to have provided the first major opportunity for biotic dispersal between the two continents. However, many dated phylogenies, especially for plant clades, show that many migrations across the Panamanian isthmus region predate even the earlier estimated timing of the closure of the isthmus (Cody et al., 2010; Pennington & Dick, 2010). Examples include three migrations from Burseraceae that moved into South America between 52 and 24 Ma (Weeks et al., 2005) and some migrations of Annonaceae that arrived in South America between 51 and 16 Ma (Pirie et al., 2006). Other migrations occurred after Farris et al.'s (2011) estimate for the timing of the land bridge formation, but before the suggested 3.4–3.1 Ma closure date; an example is the arrival of *Ruprechtia* C. A. Mey. in Central America from South America ca. 4 Ma (Pendry, 2004). For plants at least, it seems that pre-Isthmian migrations by long-distance, over-water dispersal played a greater role than previously supposed and that the emergence of the Panamanian isthmus had less of an impact than was previously assumed (Cody et al., 2010; Hughes et al., 2013).

FLORISTIC STUDIES OF THE CHOCÓ AND THEIR BIOGEOGRAPHIC IMPLICATIONS

Gentry (1982b) noted the markedly stronger floristic affinities between the rainforests of the Chocó biogeographical province and Central America than with the geographically closer rainforests of Amazonia, a view corroborated by later studies of Zamora et al. (2004) and Huber et al. (2008). The lesser floristic relationship with Amazonia implies that the Andes have been a greater migration barrier than the Pacific Ocean for the Chocó flora, or that there has been frequent overland migration between the Chocó and Central America since the closure of the Isthmus of Panama. However, there are few studies of population genetics or phylogenetics on the Chocó flora to test more directly the efficacy of the Andes as a migration barrier. The isolation of clades on either side of the cordillera (e.g., Pirie et al., 2006; see above) implies that the mountains acted as an isolating barrier in some groups. Jørgensen and León-Yánez (1999) noted that 30% of the vascular plant species in the lowland forests of Ecuador can be found on either side of the mountain belt, but without population genetic and phylogeographic studies it is impossible to infer whether these species distributions represent vicariance of ancient, widespread pre-Andean orogeny distributions, or more recent dispersal across the cor-

dillera. More molecular biogeographic studies are required, such as that of *Ceiba pentandra* (L.) Gaertn. (Dick et al., 2007), which shows low levels of genetic divergence between populations found to the east and to the west of the mountain belt. *Ceiba pentandra* is water- and wind-dispersed, which, together with low genetic divergence, indicate the likelihood for cross-Andean dispersal (Dick et al., 2007).

Gentry (1982b) also indicated stronger floristic affinities between Amazonia and eastern Panama than there are between Amazonia and the Chocó. Floristic affinity between Amazonia and Panama implies migration through Caribbean coastal regions to the north of the Andes. The plausibility of this northern route was underlined by Dick et al. (2005), who noted that 61% of the tree species in the forests of the Panama Canal watershed have conspecific populations to the west of the Eastern Andean Cordillera. However, recently Honorio et al. (2014) have presented population genetic data suggesting that only species capable of tolerating a degree of seasonal drought and surviving in the drier vegetation formations of northern South America may have been able to use this migration route. This calls into question whether it could have been used by taxa adapted to the ever-wet climates of the Chocó biogeographical province.

DUSSIA AS A BIOGEOGRAPHIC MODEL FOR THE CHOCÓ

Dussia is a genus of trees confined to tropical rainforests and distributed from southern Mexico to Bolivia and Amazonian Brazil, and on a number of the islands of the Lesser Antilles (Rudd, 1963; Zamora et al., 1999). The most recent taxonomic revision by Rudd (1963) recognized 10 species of *Dussia*, but noted that the delimitation of taxa was "tentative" because of insufficient material. A forthcoming taxonomic revision (Pennington et al., in prep.) is likely to recognize up to eight new species largely based on collections made in the past five decades. The highest species diversity for the genus is in Costa Rica (Zamora, 2010).

Dussia species are found in the Chocó biogeographical province and in Central American and Amazonian rainforests. The fact that the genus is restricted to wet lowland rainforests makes it an ideal model group to examine the biogeographic affinities of the Chocó flora.

In this paper, we present a dated phylogenetic hypothesis for *Dussia* based on nuclear ribosomal DNA internal transcribed spacers (ITS) and the chloroplast DNA (cpDNA) regions *trnL* and *trnD-T*. We use the dated phylogeny to examine the relationships of *Dussia* species found on either side of the Andes, in Amazonia, in the Chocó, and Central America. We also use it to examine the effects of the Andean uplift and the closure of the Panamanian isthmus on *Dussia* diversification. In particular, we consider the implications of our results for understanding the biogeography of the Chocó.

MATERIALS AND METHODS

TAXON SAMPLING

A total of 35 accessions representing ca. 14 species of *Dussia* were sampled (Table 1; note that several of these species await description). The low number of accessions per species partly reflects the difficulty of field collection of *Dussia* trees, which reach 50 m and are often found at very low frequencies. Five accessions representing all three of the species (two of which are new to science and await description) found in the Chocó biogeographical province were sampled from northern Ecuador, and sampling elsewhere covered most of the range of *Dussia*, enabling analysis of the biogeography of the genus and the relationships of the Chocó species.

The genera used as outgroups for this study were a broad sample from basally divergent clades of subfamily Papilionoideae shown by previous studies (Ireland et al., 2000; Wojciechowski et al., 2004) to be related to *Dussia*. They are *Ateleia*

(DC.) Benth., *Cyathostegia* (Benth.) Schery, *Angylocalyx* Taub., *Dipteryx* Schreb., *Amburana* Schwacke & Taub., and *Myrospermum* Jacq. The same six genera form the outgroup of each matrix analyzed. The sequence data for those genera were not always from the same accessions for different loci.

DNA EXTRACTION AND POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION

DNA was extracted from leaf material dried in silica gel. DNA extractions were performed according to a modification of Doyle and Doyle's (1987) CTAB method or using the DNeasy Qiagen Kit (Qiagen Ltd., Manchester, U.K.).

The forward primer ITS-5a (5′CCT TAT CAT TTA GAG GAA GGA G3′—22 bp) was used with the reverse primer ITS-4 (5′TCC TCC GCT TAT TGA TAT GC3′—20 bp) to amplify the ITS region. PCR used a 2 min. denaturing step at 94°C, followed by 39 cycles of 30 sec. at 94°C (denaturation), 1 min. at 52°C (annealing), 2 min. at 72°C (extension), and further extension for 7 min. at 72°C.

For PCR amplification of the *trnD-T* region, the primers used were C017F (5′ACC AAT TGA ACT ACA ATC CC3′—20 bp) for forward and C017R (5′CTA CCA CTG AGT TAA AAG GG3′—20 bp) for reverse from Demesure et al. (1995). PCR involved a 1 min. denaturing step at 94°C, followed by 29 cycles of 1 min. at 94°C (denaturation), 1 min. at 54°C (annealing), 3 min. at 72°C (extension), and followed by further extension for 10 min. at 72°C. After successful PCR amplification, PCR products were purified using ExoSAP IT (GE Healthcare, Affymetrix UK Ltd., High Wycombe, U.K.).

SEQUENCING

The ITS region was sequenced using a BigDye Mix (Applied Biosystems, Life Technologies Ltd., Paisley, U.K.) with the same primers (ITS-5a forward and ITS-4 reverse). The *trnD-T* region was sequenced using four primers: the reverse (C017R) primer, the internal forward primer trnDi (5′-CCA CGA TCA ACT TCC TTT CG-3′—20 bp), the internal reverse primer trnDir (5′-CGG CAA ACC AAT CAT TCC C-3′—19bp), and the forward primer trnDT.1f (5′-TTT CGA TTT TAG ATT AGA ATT GTC TTG-3′—27 bp). Sequencing PCR used 25 cycles of 30 sec. at 95°C (denaturation), 20 sec. at 50°C (annealing), and 4 min. at 60°C (extension).

SEQUENCE EDITING AND ALIGNMENT

Sequences were edited using Sequencher Vers. 4.7 (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A.). The assembled contigs were imported into Bio-Edit Vers. 7.0.5. Sequences for some outgroups were downloaded from GenBank. ClustalW (Larkin et al., 2007) was used as a preliminary alignment tool, after which the sequences were aligned manually. Indel coding was applied to all three matrices following Simmons and Ochoterena (2000). The combined chloroplast analysis of the two regions *trnL* and *trnD-T* included 65 coded indels, while the combined ITS-chloroplast analysis included a total of 104 coded indels.

PHYLOGENETIC ANALYSIS

Maximum parsimony. Each of the three data sets (ITS, combined cpDNA [*trnL* and *trnD-T*], and combined ITS-cpDNA) was subject to preliminary analysis using maximum parsimony. Maximum parsimony analysis used PAUP*4.0b10 (Swofford, 2003) with all characters unordered and unweighted. For each data set two heuristic searches were conducted. The first search performed 1000 random addition sequence replicates and held 10 trees per replicate, implementing TBR (tree-bisection-reconnection) branch swapping, but not MulTrees and steepest descent. The trees saved from this first search became the starting trees for the second search, which implemented TBR and MulTrees and saved a maximum of 5000 trees. Bootstrap analysis was used to evaluate the

TABLE 1 Voucher specimen information.

Taxon	Voucher details	Country	Locality	Herbarium	GenBank ITS	GenBank *trnL*	GenBank *trnD-T*
Dussia sp. indet. 1	*R.T. Pennington 624*	Costa Rica	Puntarenas: Canton de Buenos Aires, Parque Internacional La Amistad, Sector Pacifico	E, INB	KJ813641	KJ813676	KJ813711
Dussia sp. indet. 2	*R.T. Pennington 685*	Colombia	Antioquia: Autopista Medellin-Bogota	E, COL, JAUM	KJ813645	KJ813680	KJ813715
Dussia sp. indet. 3	*R.T. Pennington 310*	Ecuador	Sucumbios: 34km above Lumbaqui	E, QCNE	KJ813620	KJ813655	KJ813690
Dussia sp. indet. 4	*R.T. Pennington 667*	Ecuador	Zamora	E, QCNE	KJ813644	KJ813679	KJ813714
Dussia Krug & Urb. ex Taub. sp. nov. A1	*R.T. Pennington 569*	Costa Rica	Puntarenas: Osa Peninsula, Canton de Osa, Playa Chal	E, INB	KJ813631	KJ813666	KJ813701
Dussia sp. nov. A2	*R.T. Pennington 632*	Costa Rica	Puntarenas: Golfito, El Refugio Nacional de Vida Silvestre Golfito	E, INB	KJ813642	KJ813677	KJ813712
Dussia sp. nov. B	*R.T. Pennington 574*	Costa Rica	Puntarenas: Osa Peninsula, Canton de Osa, Cerro Chocuaco	E, INB	KJ813633	KJ813668	KJ813703
Dussia sp. nov. C1	*R.T. Pennington 696*	Colombia	Antioquia: Rd. Medellin–Rio Negro	E, COL, JAUM	KJ813646	KJ813681	KJ813716
Dussia sp. nov. C2	*R.T. Pennington 704*	Colombia	Antioquia: Rd. La Union to Mesopotamia	E, COL, JAUM	KJ813647	KJ813682	KJ813717
Dussia sp. nov. D1	*R.T. Pennington 544*	Ecuador	Los Rios	E, QCNE	KJ813626	KJ813661	KJ813696
Dussia sp. nov. D2	*R.T. Pennington 546*	Ecuador	Los Rios: Rio Palenque Biological Station	E, QCNE	KJ813627	KJ813662	KJ813697
Dussia sp. nov. E1	*R.T. Pennington 530*	Ecuador	Napo: Canton Orellana, Parque Nacional Yasuni	E, QCNE	KJ813624	KJ813659	KJ813694
Dussia sp. nov. E2	*R.T. Pennington 538*	Ecuador	Napo: Canton Orellana, Parque Nacional Yasuni	E, QCNE	KJ813625	KJ813660	KJ813695
Dussia sp. nov. F	*R.T. Pennington 559*	Ecuador	Carchi	E, QCNE	KJ813630	KJ813665	KJ813700
Dussia sp. nov. G1	*R.T. Pennington 573*	Costa Rica	Puntarenas: Osa Peninsula, Canton de Osa, Cerro Chocuaco	E, INB	KJ813632	KJ813667	KJ813702
Dussia sp. nov. G2	*R.T. Pennington 582*	Costa Rica	Puntarenas: Osa Peninsula, Canton de Golfito, Parque Nacional Corcovado	E, INB	KJ813634	KJ813669	KJ813704
D. atropurpurea N. Zamora, R.T. Penn. & C. H. Stirt. 1	*R.T. Pennington 611*	Costa Rica	Guanacaste: Parque Nacional Guanacaste	E, INB	KJ813639	KJ813674	KJ813709

D. atropurpurea 2	*R.T. Pennington 620*	Costa Rica	Guanacaste: Canton de Upala	E, INB	KJ813640	KJ813675	KJ813710
D. [illegible] (Benth.) Amshoff	*S. Mori [illegible]*	French Guiana	Inini: Saul & vic	NY	KJ813619	KJ813654	KJ813689
D. lehmannii Harms 1	*R.T. Pennington 554*	Ecuador	Pichincha: Pedro Vicente Maldonaldo	E, QCNE	KJ813629	KJ813664	KJ813699
D. lehmannii 2	*R.T. Pennington 550*	Ecuador	Pichincha: Primary forest reserve on land of Fundacion Florestal Dunn at Rio Pitzara	E, QCNE	KJ813628	KJ813663	KJ813698
D. macrophyllata (Donn. Sm.) Harms 1	*R.T. Pennington 601*	Costa Rica	Puntarenas: Monteverde	E, INB	KJ813636	KJ813671	KJ813706
D. macrophyllata 2	*R.T. Pennington 606*	Costa Rica	Guanacaste: Estación San Ramón	E, INB	KJ813637	KJ813672	KJ813707
D. macrophyllata 3	*R.T. Pennington 608*	Costa Rica	Guanacaste: Parque Nacional Guanacaste	E, INB	KJ813638	KJ813673	KJ813708
D. [illegible] (Donn.) Harms	*R.T. Pennington 595*	Costa Rica	Heredia: La Selva Biological Station	E, INB	KJ813635	KJ813670	KJ813705
D. tessmannii Harms 1	*R.T. Pennington 516*	Ecuador	Napo: Cantón Tena, near Estación Biológica Jatun Sacha	E, QCNE	KJ813621	KJ813656	KJ813691
D. tessmannii 2	*R.T. Pennington 516*	Ecuador	Napo: Cantón Tena, near Estación Biológica Jatun Sacha	E, QCNE	KJ813622	KJ813657	KJ813692
D. tessmannii 3	*R.T. Pennington 522*	Ecuador	Napo: Cantón Tena, near Estación Biológica Jatun Sacha	E, QCNE	KJ813623	KJ813658	KJ813693
D. tessmannii 4	*R.T. Pennington 641*	Ecuador	Napo: Canton Tena, near Estación Biológica Jatun Sacha	E, QCNE	KJ813643	KJ813678	KJ813713
Amburana cearensis (Allemão) A. C. Sm.	*S. G. Bridgwater 1011*	Brazil	Bahia	E	KJ813615	KJ813648	KJ813683
Angylocalyx Taub. sp.	*Pennington s.n.*	U.K.	Kew living collection	K	KJ813616	KJ813649	KJ813684
Ateleia albolutescens Mohlenbr.	*Linares 4330*	Mexico	Mexico: Chiapas, Cintalapa	K	GU219993	KJ813650	KJ813685
Cyathostegia mathewsii (Benth.) Schery	*R.T. Pennington 657*	Ecuador	Loja	E	HM347452	KJ813651	KJ813686
Dipteryx alata Vogel	*R.T. Pennington 494*	Brazil	Goiás	E	KJ813617	KJ813652	KJ813687
Myrospermum sousanum A. Delgado & M. C. Johnst.	*Bell s.n.*	U.K.	Kew living collection	K	KJ813618	KJ813653	KJ813688

Abbreviations: COL = Universidad Nacional de Colombia; E = Royal Botanic Garden Edinburgh; INB = Instituto Nacional de Biodiversidad; JAUM = Jardín Botánico Joaquín Antonio Uribe; K = Royal Botanic Gardens, Kew; NY = New York Botanical Garden; QCNE = Museo Ecuatoriano de Ciencias Naturales.

internal dataset support for clades. A heuristic search was performed based on fast-stepwise analysis of 10,000 bootstrap replicates. TBR branch swapping and MulTrees were selected and no more than five trees were saved per replicate.

Bayesian analysis. Bayesian analysis used MrBayes Vers. 3.1 (Ronquist et al., 2005) with a general time reversible (GTR) model with site heterogeneity gamma distributed and with invariant sites. Each analysis ran for one million generations with a sample frequency of 100. A burn-in of 25% was implemented and trees were summarized in a 50% majority rule consensus topology. Consensus trees were viewed and modified for graphical presentation using FigTree Vers. 1.3.1 (Rambaut, 2009).

Phylogenetic dating analysis. Phylogenetic dating of combined ITS-chloroplast sequence data used BEAST (Bayesian evolutionary analysis sampling trees) Vers. 1.4.8 (Drummond & Rambaut, 2007). A Nexus file of the combined ITS-chloroplast sequence data without indel-coding was imported into BEAUti (Bayesian evolutionary analysis utility). Calibration points were defined using dates calculated in an evolutionary rates analysis of Leguminosae (Lavin et al., 2005). Ages of 47 Ma were applied to the root of the phylogeny, and the crown node of the clade containing *Dussia*, *Angylocalyx*, *Amburana*, *Dipteryx*, and *Myrospermum* was assigned an age of 38 Ma. These were the minimum ages for these nodes calculated by Lavin et al. (2005; nodes 14 and 16 in that study). The minimum age constraints were used, as opposed to mean or maximum ages, because we wished to bias toward younger dates to test more rigorously the hypotheses of the Andes as a barrier, and that migration between South and Central America required the Panamanian isthmus land bridge. If an age of disjunction across the Andes is calculated as old enough to be caused by the rising mountains when that age is biased young, it provides a stronger indication of a phylogenetic split caused by the mountains. Similarly, if such a biased date for a migration event across the isthmus predates 3 Ma, when the isthmus closed, this is strong evidence for over-water dispersal. Each calibrated node was profiled. A GTR, gamma and invariant site heterogeneity model was selected with a relaxed uncorrelated lognormal model. Because a secondary calibration was used, a normal prior distribution was selected, as recommended by Ho (2007), and the calibration ages were added under a normal mean label. The tree prior model chosen was Yule. The MCMC was run for 50 million generations, sampling every 10,000. BEAST analyses were run through the CBSU Web Computing Resources portal website (Cornell University, 2009). Trees were processed using Tree Annotator (Drummond & Rambaut, 2007), and trees were viewed in FigTree (Rambaut, 2009).

RESULTS

ITS

The total length of the aligned ITS matrix was 840 characters, of which 165 were parsimony informative with 39 parsimony informative coded gaps. The most parsimonious trees had a length of 504 steps, with a consistency index of 0.756 and a retention index of 0.695. Bayesian analysis of the ITS sequence data resulted in a very similar tree topology (Fig. 1).

COMBINED CPDNA

The combined plastid matrix had 2593 characters, of which 130 were informative with 65 parsimony informative coded gaps. The most parsimonious trees had a length of 406 steps with a consistency index of 0.847 and a retention index of 0.793. The maximum parsimony strict consensus tree topology is similar to that of the ITS analysis, but was marginally more resolved. Bayesian analysis of the combined chloroplast sequence data resulted in a tree topology that was similar to but more resolved than the parsimony analysis

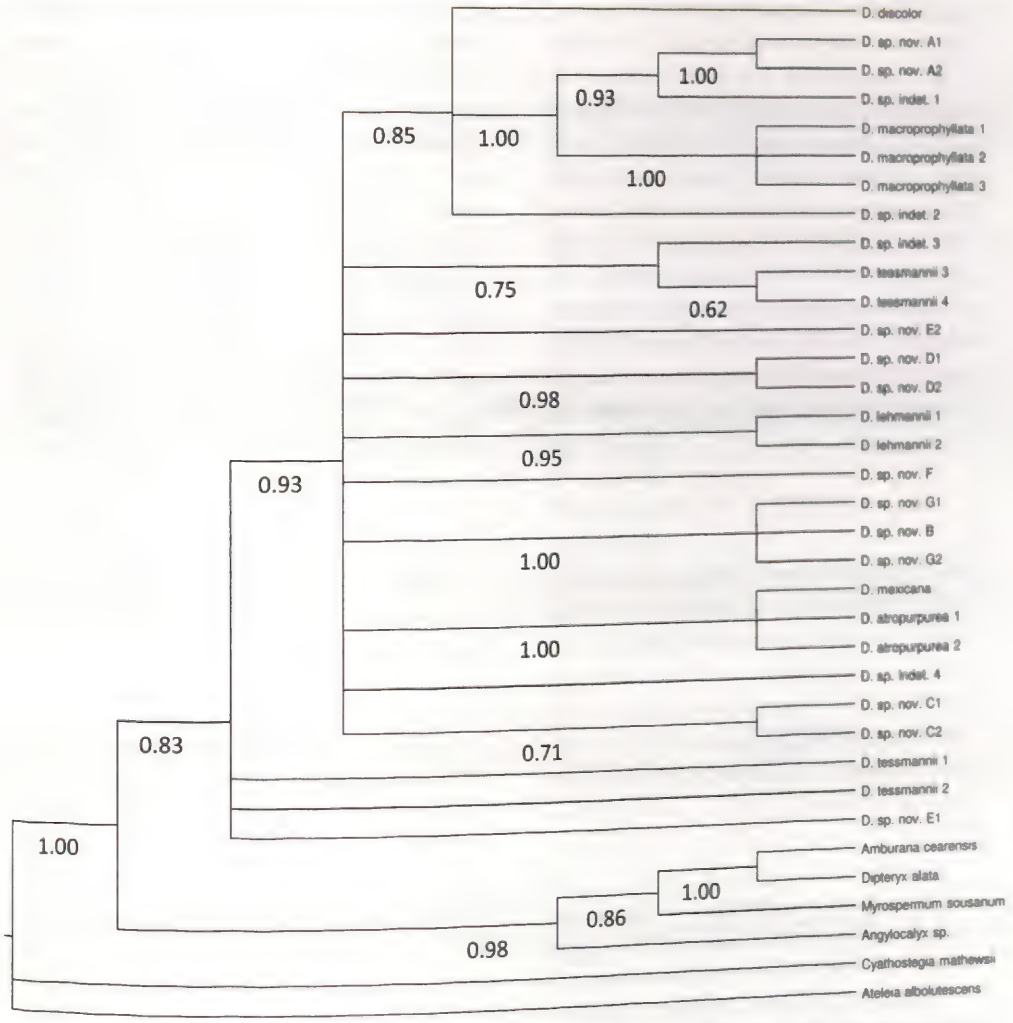

FIGURE 1. Fifty percent majority rule consensus tree produced from Bayesian analysis of ITS sequence data, with posterior probability values below the branches.

and with a distinct division between the clades from east of the Andes and those from the west (Central America, the Chocó, and Colombian inter-Andean valleys; Fig. 2).

PHYLOGENETIC CONGRUENCE BETWEEN ITS AND CPDNA

The only instance of strongly supported incongruence involved the three samples of *Dussia macroprophyllata* (Donn. Sm.) Harms (RTP601, 606, and 608). In the ITS analyses they formed a clade (Fig. 1), but in the chloroplast analyses they were resolved in two separate groups because *D. macrophyllata* RTP601 emerged in a second Costa Rican clade (Fig. 2). This incongruence might possibly suggest a hybridization event followed by subsequent introgression, which can mislead inference of a species tree (e.g., Doyle, 1992). However, because of the restricted nature of the incongruences and because the variable

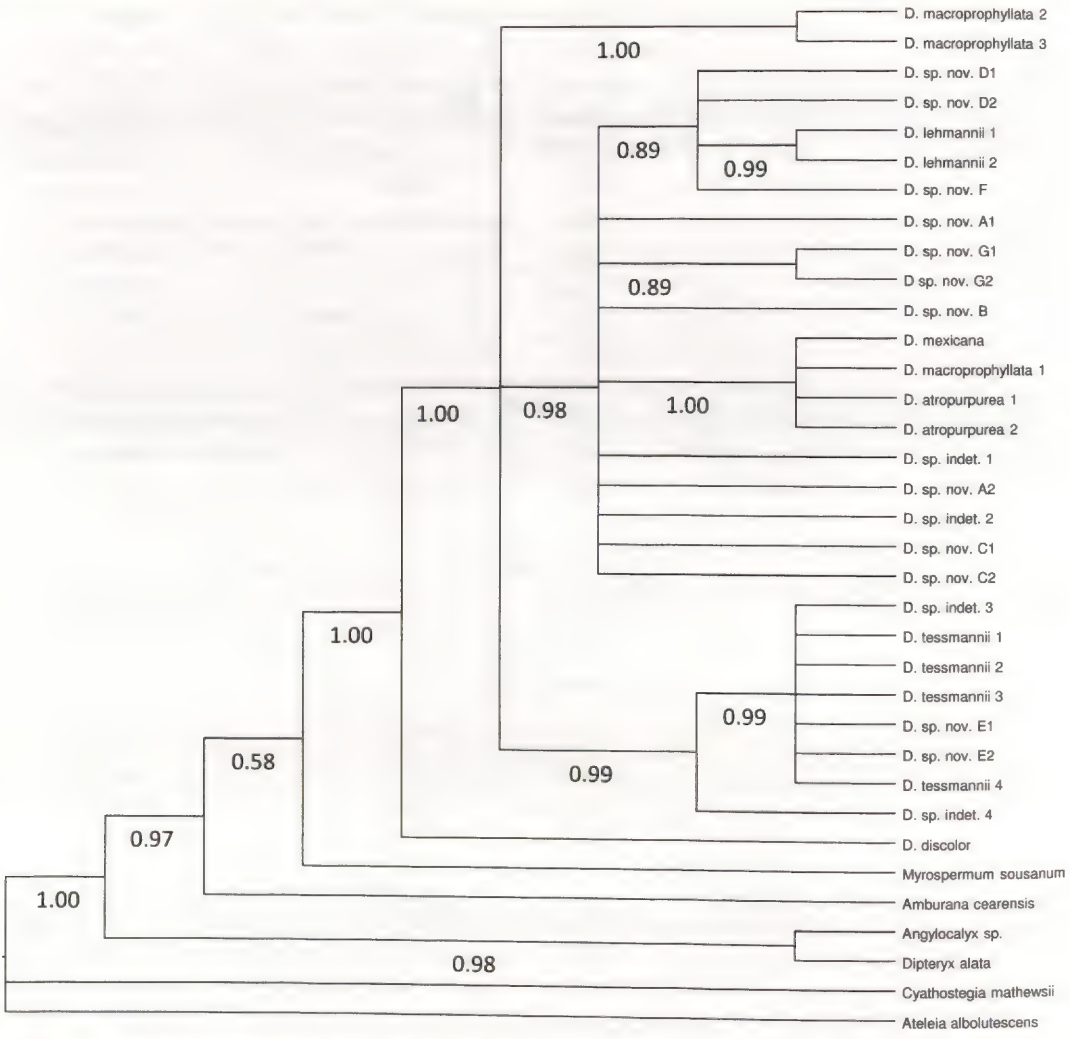

FIGURE 2. Fifty percent majority rule consensus tree produced from the Bayesian analysis of the combined chloroplast data sets *trnL* and *trnD-T*, with posterior probability values below the branches.

phylogenetic placements of the Costa Rican accessions involved would not affect our overall biogeographic conclusions (e.g., those concerning the relationships of the Chocó accessions), we combined our datasets for subsequent analyses to maximize information.

COMBINED ITS-CPDNA

The most parsimonious trees had a length of 931 steps with a consistency index of 0.779 and a retention index of 0.707. The parsimony strict consensus tree was more resolved than either of the ITS or combined chloroplast analyses, and with higher bootstrap support values for clades. This increase in resolution suggests complementary phylogenetic signals in the nuclear and chloroplast datasets, again suggesting that problems of incongruence across the dataset are minimal. Bayesian analysis of the combined ITS-chloroplast sequence data resulted in a tree topology that was

congruent but more resolved than the maximum parsimony consensus trees. There is a clear division between the clades from east of the Andes and those found elsewhere (Fig. 3). The accessions of Chocó species (*Dussia lehmannii* Harms, *Dussia* sp. nov. D, *Dussia* sp. nov. F) are a monophyletic group, nested amongst Central American species. Finally, attention should be drawn to the three Colombian accessions: *Dussia* sp. nov. C1 (RTP696) and C2 (RTP 704), and *Dussia* sp. indet. 2 (RTP685). These are found within two separate inter-Andean valleys, the Ríos Cauca (*Dussia* sp. nov. C1, C2) and Magdalena (sp. indet. 2), and the accessions from each valley are grouped separately with Central American species.

DATED PHYLOGENY

The BEAST analysis of the combined ITS-chloroplast data resulted in a tree topology similar to the other phylogenetic analyses. There are clear geographical groups from the east and west of the Andes (Fig. 4). The date for the crown node of *Dussia* is 19.46 (7.65–31.47) Ma (Fig. 4, node A). This implies that *Dussia* was diversifying when the tropical Andes were a fraction of their current altitude and confirms the genus was a good case study example for testing the effects of the Andean orogeny. A split between west and east of the Andes occurred at node B, 15.19 (5.94–25.18) Ma.

DISCUSSION

THE ANDES AS A BARRIER

The combined ITS and chloroplast phylogeny shows clear geographic structure, with a split across the Andes. All species found to the west of the Andes (Central America, Colombian inter-Andean valleys, and the Chocó) are placed in a monophyletic group, albeit with relatively weak support. Sister to this group is a well-supported clade containing all accessions from Amazonia, and sister to all other *Dussia* species is an accession of *D. discolor* (Benth.) Amshoff from French Guiana. The dated phylogeny gives a divergence date of ca. 15 Ma for the stem group of the clade of accessions found west of the Andes (Fig. 4, node B). Given that this date may be an underestimate (due to the bias toward younger ages in the analysis) and that the Western Cordillera of the Central Andes had reached no more than half of their present height by 25–18 Ma and the Eastern Cordillera of the Central Andes had only reached a maximum of half its present height by 10 Ma (Gregory-Wodzicki, 2000), the indications are that the Andes presented a barrier to *Dussia* even when they were only about half their current altitude.

THE CLOSURE OF THE ISTHMUS OF PANAMA

The earliest migration between South America and Central America on the *Dussia* tree is dated at ca. 15 Ma at the stem node and ca. 13 Ma at the crown node (Fig. 4, node C), which substantially predates initial estimates for the date of formation of the Panamanian land bridge (Coates & Obando, 1996) but overlaps with more recent suggested dates (Farris et al., 2011; Montes et al., 2012). The Chocó clade is nested in the Central American clade. This suggests that subsequent to the south-north migration event between South and Central America, a north-south migration event must have occurred ca. 7 Ma (Fig. 4, node D). Because the accessions from Colombian inter-Andean valleys are not placed in the same group as the Chocó species, the phylogeny indicates other migrations between Central and South America, but the lack of strong support for the relationships within the wider clade of accessions found to the west of the Andes precludes clear indications of directionality.

What is clear is that this dated phylogeny for *Dussia* shows there were multiple migrations between South and Central America, some of which occurred before the widely accepted (e.g., Coates & Obando, 1996) estimates for the timing of land bridge formation ca. 3 Ma. We can be confident

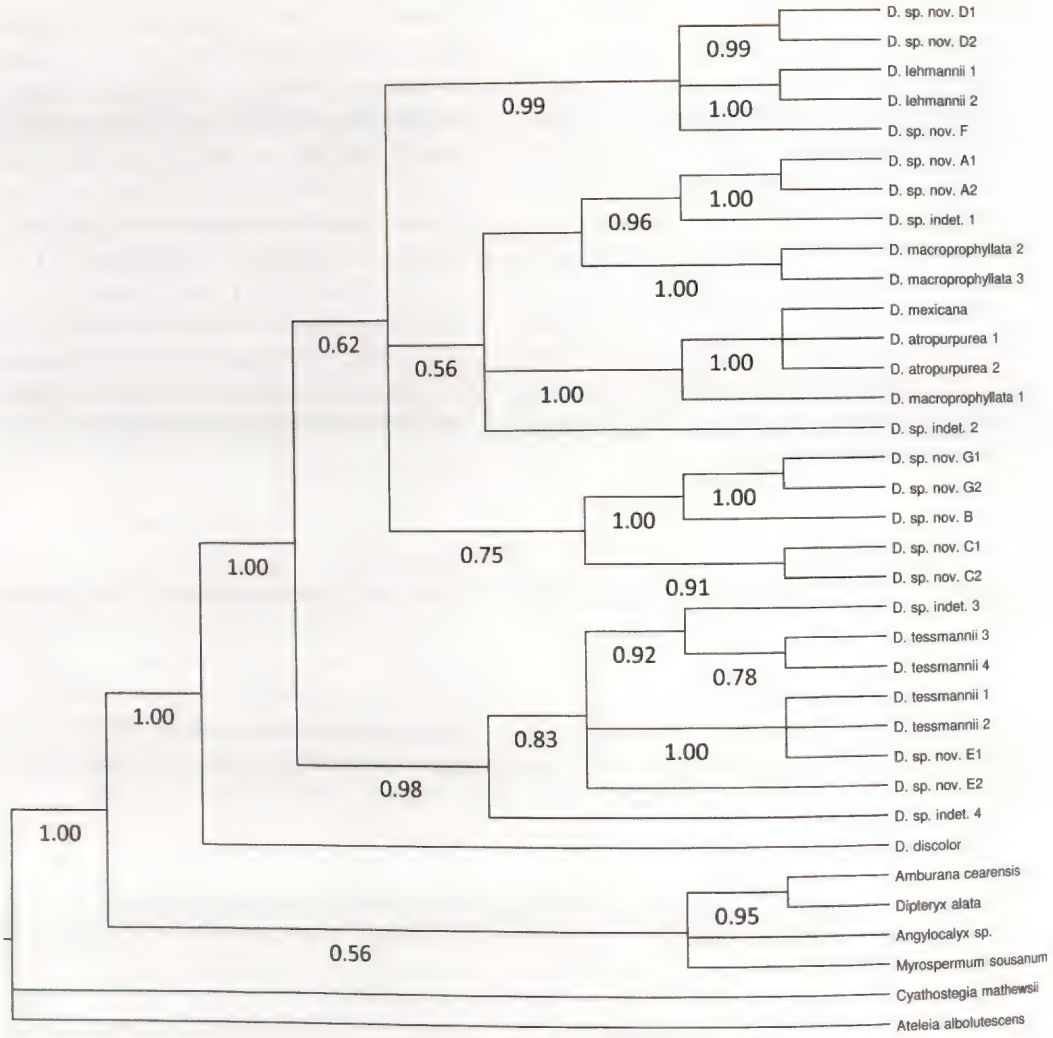

FIGURE 3. Fifty percent majority rule consensus tree produced from the Bayesian analysis of the combined ITS and chloroplast *trnL* and *trnD-T* data sets, with posterior probability values below the branches.

of this inference because the analysis was biased to young dates. It is of note that *D. martinicensis* Krug & Urb. ex Taub. (not sampled here) is found on several islands in the Lesser Antilles. Therefore, in spite of *Dussia*'s probable dispersal mechanism by specialist frugivores such as primates (Zamora et al., 1999), it has undoubtedly dispersed long distances across water successfully between South and Central America, possibly on several occasions, and in both directions.

COLOMBIAN INTER-ANDEAN VALLEYS

The relationships of the accessions from the valleys of the Ríos Cauca (*Dussia* sp. nov. C1, C2) and Magdalena (*Dussia* sp. indet. 2), which are resolved separately in the tree, is an indication of both isolation within these valleys and a complex history of floristic exchange between Central America and Colombian inter-Andean valleys. At the north end of the Western Cordillera, the Magdalena and Cauca valleys run into lowland

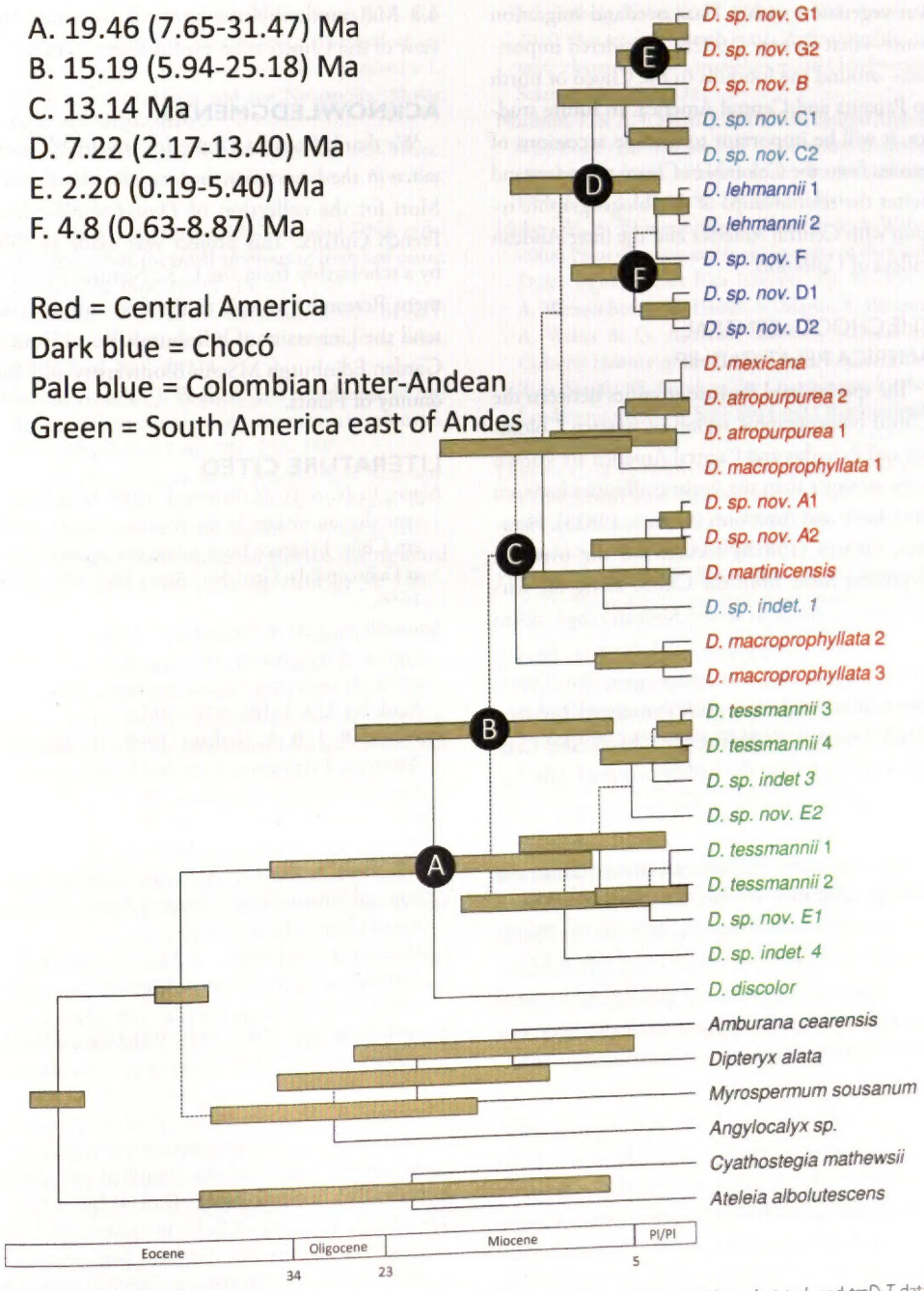

FIGURE 4. Maximum clade credibility tree from the BEAST analysis of the combined ITS and chloroplast *trnL* and *trnD-T* data sets, with node dates in millions of years. This tree summarizes the node height and rate statistics with the maximum sum of posterior probabilities on its n–2 internal nodes. Nodes discussed in the text are labeled A to F. Dashed lines represent branches that have a posterior probability of < 0.95. Pl/Pl = Pliocene/Pleistocene.

wet vegetation with a clear overland migration route—that Gentry (1982b) considered important—around the foothills to the Chocó or north to Panama and Central America. In future studies, it will be important to include accessions of species from the Colombian Chocó to understand better the relationships of this biogeographic region with Central America and the inter-Andean valleys of Colombia.

THE CHOCÓ–CENTRAL AMERICA RELATIONSHIP

The species-level floristic affinities between the Chocó biogeographic region of western Colombia and Ecuador and Central America are known to be stronger than the floristic affinities between the Chocó and Amazonia (Gentry, 1982b). However, Gentry (1982b) focused on the overland migration route from the Chocó along the narrow strip to the west of the Andean range, north into Panama, Costa Rica, and beyond. As discussed above, the dated phylogeny for *Dussia* shows that migration events occurred between South America, including the Chocó, and Central America before the widely accepted date (ca. 3 Ma) of land bridge formation, so over-water dispersal seems possible.

The phylogeny of *Dussia* clearly demonstrates stronger affinities of the Chocó with Central America than with Amazonia because the Pacific Ecuador accessions are nested in a Central American clade. In contrast, the phylogeny suggests that there have been no trans-Andean migrations between Amazonia and the Chocó region. While the migrations between the Chocó and Central America may not have been over land as envisaged by Gentry (1982b), our phylogeny corroborates his view of strong floristic links between these areas. In addition, for the Chocó, Gentry (1982b: 114) postulated "autochthonous recent evolution of its strikingly endemic biota." The placement of the three *Dussia* species endemic to the Chocó in a recent (stem, 7.2 Ma, crown, 4.8 Ma) monophyletic group corroborate this view of the Chocó as an evolutionary cradle.

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